A NOTE ON THE INHERITANCE OF EYE PATTERN IN BEANS AND ITS RE-LATION TO TYPE OF VINE[1]

FRANK M. SURFACE

In a recent paper (Pearl and Surface, 1915) from this laboratory two varieties of yellow-eyed beans were described and figured under the somewhat provincial names of Improved Yellow Eye and Old-Fashioned Yellow Eye. The type of eye pattern characteristic of each of these varieties is shown below in Figs. 1 and 2. On the Improved Yellow Eye the colored area covers about one fourth the area of the bean. The outer border of the eye pattern is clear-cut and regular, with very little or no spotting on the remainder of the bean.

The Old-Fashioned Yellow Eye pattern (Fig. 2) is much smaller in area and is quite irregular in outline but nevertheless very definite. It consists of at least three color centers: (1) A posterior[2] spot covering the caruncle and extending at least part way around the hilum. Laterally this area is extended into two rather broad wings which reach as far forward as the micropyle. (2) An anterior spot surrounding the micropyle, and (3) an anterior stripe which may or may not connect with the micropyle spot.

In connection with other work a number of crosses have

[1] Papers from the Biological Laboratory of the Maine Agricultural Experiment Station, No. 99.

[2] The *posterior* end of a bean is that end of the hilum at which the caruncle lies. It is the end opposite the micropyle.

been made between these two varieties. Something over 40 cross-pollinated beans have been secured. Of these, 15 have been grown at least as far as the F_1 generation. These 15 plants gave a total of 295 F_1 beans. Except for some minor fluctuations these F_1 beans were all alike, but differed markedly from either parent. In the notes these F_1 beans have been designated "Piebald" because of the very irregular spotted pattern. Fig 3 shows a typical piebald pattern. In addition to the spotting these beans differ from the Improved Yellow Eye in having a very irregular outline to the colored area. While the pattern is somewhat variable, there is never any difficulty in distinguishing this from the typical Improved Yellow Eye pattern.

FIG. 1. Typical Improved Yellow Eye color pattern.

FIG. 2. Typical Old-Fashioned Yellow Eye color pattern.
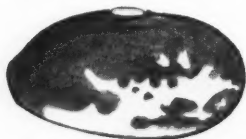

FIG. 3. Typical "piebald" color pattern occurring on the F_1 beans of a cross between the Improved and Old-Fashioned Yellow Eye types.

Up to the present time only a few of these hybrids have been carried to the F_2 generation. However, enough have been obtained to show that these piebald beans give both parent types and also more beans with the piebald pattern. It is very probable that only these three types occur in the F_2 and later generations.

While the data so far obtained from hand-pollinated hybrids are not sufficiently extensive to warrant further discussion, certain other data have been obtained which have a bearing on this subject.

In 1911 and 1912 the Experiment Station grew a number of plots planted with different strains and varieties of beans. Among these were a number of strains of Improved and Old Fashioned Yellow Eye. In some cases plots of these two varieties were located near each other. Seed from some of the 1911 plots were planted in 1912.

A considerable number of plants in these plots showed
that the seed had been cross-pollinated by bumble-bees the
year before. Among the plants in the Yellow Eye plots
there were a number which bore typical piebald beans
similar to that shown in Fig. 3. Some of these piebald
plants were harvested separately and their progeny con-
tinued in a small way inside a screened cage. By the
spring of 1915 it had been ascertained that a cross be-
tween an Improved and an Old-Fashioned Yellow Eye
resulted in such a piebald pattern. Accordingly a con-
siderable number of these piebald beans were grown in
1915. The following paper is based upon the data from
these natural hybrids.

Table I gives the detailed data relative to the offspring

TABLE I
Showing the Segregation in the Progeny of Piebald Beans

Pedigree No.	Year	Row	Piebald	I. Y. E.	O. F. Y. E.
1294–5	1912	30	11	3	4
	1913	87	—	3	2
		88	5	—	—
	1914	31	4	—	—
	1915	58	2	3	4
		269	12	7	3
		270	7	2	5
		271	8	1	3
		272	10	3	1
		273	6	—	2
		274	6	3	6
Total for 1294–5			*71*	*25*	*30*
1311	1913	104	3	—	—
	1914	32	2	1	2
	1915	292	13	7	4
		295	10	4	5
		296	6	1	3
		297	3	2	3
Total for 1311			*37*	*15*	*17*
153 X	1915	303	5	3	4
		304	8	1	3
Total for 153 X			*13*	*4*	*7*
1318	1915	307	5	2	5
		308	5	1	4
Total for 1318			*10*	*3*	*9*
1321	1915	310	8	3	3
		311	7	3	4
Total for 1321			*15*	*6*	*7*
Grand total			146	53	70

of 269 piebald beans. It will be understood that each row was planted from the offspring of a single plant. Not all of these beans can be considered as belonging to the F_2 generation. A portion of these certainly belong to the F_3 and later generations. This question will be considered further in a later paragraph.

From this table it will be seen that only three kinds of beans were obtained from these piebald seed. These were piebald, Improved Yellow Eye and Old-Fashioned Yellow Eye. This fact, in connection with the evidence obtained from controlled pollinations as noted above, makes it practically certain that these piebald beans are hybrids between these two varieties of Yellow Eye beans.

Further, with the exception of three small rows none of of these piebald beans gave evidence of breeding true. In each of these three cases some of the piebald beans have split in later generations. Thus in pedigree No. 1294–5 the 1914 Row 31 is the offspring of one of the five piebald plants in the 1913 Row 88. It seemed possible that this line was breeding true. However, the 1915 Row 58 is the offspring of a plant from Row 31 of the year before, and Row 58 gave all three types, so that both of the preceding rows must have been heterozygous. If larger numbers had been grown from the same seed they would undoubtedly have thrown all three types.

The evidence thus indicates that the piebald pattern is the expression of the heterozygous condition of the factorial difference between these two types of Yellow Eye beans. A similar conclusion was reached by von Tschermak (1912). He obtained spotted beans very similar to our "piebald" from crosses between eyed and white or eyed and solid color beans. These piebald beans were always heterozygous, throwing on the one hand a large eye with regular outline corresponding with our Improved Yellow Eye and on the other hand a small-eyed bean. Judging from his figures (p. 208) von Tschermak's small-eyed bean had nothing corresponding to the peculiar pattern on our Old-Fashioned Yellow Eye. However, in

relative quantity of pigment these beans agree very well.

Von Tschermak assumed a unifactorial difference between the large and small-eyed beans, with the spotted pattern as the heterozygote. In the F_2 generation he obtained a $1:2:1$ ratio.

Returning now to our own data as given in Table I it is clear that if the difference between the Improved and Old-Fashioned patterns is due to a single factor we should expect in the segregating generations 2 piebald: 1 I. Y. E. : 1 O. F. Y. E. The numbers obtained in Table I will hardly support this view. $146:53:70$ can hardly be looked upon as a $2:1:1$ ratio. It is true that the deviation is not so great, but that these observed numbers might be chance fluctuations from a $2:1:1$ ratio. On the theory of probability the odds against the occurrence of such a deviation are about 5 to 1.

Of the more common Mendelian ratios the observed figures are much more closely fitted by $9:3:4$. The observed and expected numbers in this case are

	Piebald	I. Y. E.	O. F. Y. E.
Observed No.	146	53	70
Expected No. on $9:3:4$ ratio......	151.3	50.4	67.3

It is clear that there is a very reasonable agreement.

Further evidence in support of the view that the segregation is not $2:1:1$ is found by examining Table I in more detail. Thus the totals for each of the five pedigrees show an excess of Old-Fashioned Yellow Eyes over the Improved type. In three of these pedigrees the number of plants is relatively small. However, the cumulative evidence makes it almost certain that the deviations are not due to chance.

It was stated above that only a portion of these plants belonged to the F_2 generation. In a bifactorial character considerable difference might be introduced by the combination of data from different generations. From the records it is known that all the plants in pedigree Nos. 153 X, 1318 and 1321, together with two rows, 104 and 292,

from pedigree 1311, belong to the F_2 generation. Taking these plants alone, we have the data given in Table II.

<div align="center">TABLE II</div>

<div align="center">Showing the Segregation in the F_2 Generation from Piebald Beans</div>

Piebald	I. Y. E.	O. F. Y. E.
54	20	27

It is seen at once that there is again the same relative excess of O. F. Y. E. over I. Y. E. that is shown by the complete data in Table I. The expectation on the $2:1:1$ ratio is $50.5:25.3:25.3$, while on the $9:3:4$ ratio the expectation is $56.8:18.9:25.3$. It will be seen that the latter figures more nearly fit the observed numbers.

A $9:3:4$ ratio presumes a bifactorial composition. However, a moment's consideration shows that such a ratio cannot have its usual significance in this case. If this were the usual bifactorial segregation, one out of every nine F_2 piebald beans ought to breed true in the third generation. Yet out of 15 rows from piebald beans which certainly belong to the F_3 or F_4 generation not a single one bred true.

Further, one half of the F_2 Old-Fashioned Yellow Eye segregates and two thirds of the F_2 Improved Yellow Eye segregates ought to show segregation in the third generation. In 1915, 43 Old-Fashioned Yellow Eye, F_3 plants were grown and every one bred true. At the same time 38 F_3 plants were grown from Improved Yellow Eye seed. Thirty-seven of these gave typical Improved Yellow Eye beans, but one plant gave piebald beans. The F_2 plant which furnished this latter seed was grown without any protection from insects in 1912 and it is very probable that the one I. Y. E. bean which gave piebald seed was due to insect pollination with Old-Fashioned Yellow Eye pollen. This is all the more probable because the ratio $1:37$ is by no means what would be expected on the usual bifactorial hypothesis.

The evidence is fairly conclusive that the I. Y. E. and the O. F. Y. E. segregates breed true and that beans with

the piebald pattern are always heterozygous. These results could be very simply interpreted on a single-factor hypothesis, but the numerical results do not fit the $2:1:1$ ratio demanded by that hypothesis.

While the data at hand are not as extensive as one might desire in order to build a complete theory, yet there is much to be said in favor of the following provisional hypothesis. Let I be a factor which in its homozygous condition II produces the Improved Yellow Eye pattern. Then Ii will be the zygotic constitution of the piebald plants and ii that of the Old-Fashioned Yellow Eye pattern. Assume further a lethal factor L independent in its segregation and of such a nature that LL in the presence of II produces a non-viable zygote. The complete F_2 segregation would then be as follows:

1	$I\ I\ L\ L$	Non-viable[3]
2	$I\ I\ L\ l$	I. Y. E.
1	$I\ I\ l\ l$	
2	$I\ i\ L\ L$	
4	$I\ i\ L\ l$	Piebald
2	$I\ i\ l\ l$	
1	$i\ i\ L\ L$	
2	$i\ i\ L\ l$	O. F. Y. E.
1	$i\ i\ l\ l$	

Such a segregation would result in the ratio 8 piebald : 3 I. Y. E. : 4 O. F. Y. E. Testing this ratio against the total observed numbers in Table I we get

	Piebald	I. Y. E.	O. F. Y. E.
Observed No.	146	53	70
Expected No. on $8:3:4$ ratio...........	143.5	53.8	71.7

It is seen that there is a very close agreement between the observed and expected numbers; much closer, in fact, than in the case of the $9:3:4$ ratio previously used.

[3] The same result would be obtained if ll in the presence II produced a non-viable zygote. This point could be determined by suitable crosses between the F_2 segregates.

In the case of known F_2 plants, as given in Table 2, the results are

	Piebald	I. Y. E.	O. F. Y. E.
Observed No.	54	20	27
Expected No. on 8 : 3 : 4 ratio	53.8	20.2	26.9

Here again there is a very remarkable agreement. In fact all of the data at hand fit into this theory very nicely. Final proof of its correctness or incorrectness can only come with more extended crossings between the segregates and with the parent stocks. Such experiments are now under way.

RELATION OF EYE PATTERNS TO TYPE OF VINE

Two years ago while going over some data from pure lines of Yellow Eye beans grown inside a screened enclosure the writer was struck by the fact that with few exceptions all of the O. F. Y. E. pure lines had the bush type of vine, while nearly all the I. Y. E. lines were classed as short runners. This point was further emphasized by the observation that in several cases the segregation from piebald beans showed that all of the O. F. Y. E. segregates were bush beans and all the I. Y. E. were runners. It was, therefore, of some interest to tabulate the data relative to type of vine in connection with the eye pattern.

The classification of plants with reference to type of vine has usually been made at the time of harvest. In some years the plants grown inside the screened cage have been classified as to vine type shortly before harvest. In either case the plants were mature or practically so. The plants grouped under the term "bush" are those which show determinate growth, terminal inflorescence, and lack the ability to twine about supports. The "runner" plants show axillary inflorescence and the twining habit (circumnutation). All of the runner beans considered in this paper are of the short runner or short pole type, rarely reaching a total height of more than 125 cen-

timeters. Usually they develop few branches. Under ordinary conditions such beans do not show indeterminate growth. However, from the investigations of Emerson (1916) it is probable that they would do so if growth were not stopped by unfavorable conditions or excessive seed production.

Data as to type of vine are available from 247 of the plants given in Table I. Table III shows the distribution of the type of vine for each of the three eye patterns. The data for each pedigree number are summarized separately.

TABLE III

DISTRIBUTION OF TYPE OF VINE FOR EACH OF THE THREE EYE PATTERNS

Pedigree No.	Piebald		I. Y. E.		O. F. Y. E.	
	Runner	Bush	Runner	Bush	Runner	Bush
1294–5	40	19	12	6	0	27
1311	18	19	4	11	0	17
153 X	3	10	2	2	0	7
1318	0	10	0	3	0	9
1321	9	6	6	0	0	7
Total	70	64	24	22	0	67

The most striking thing in connection with this table is the complete absence of runner vines among the Old-Fashioned Yellow Eye beans. Apparently the gene for bush type of vine is closely associated with the gene for the Old-Fashioned Yellow Eye pattern. That this association is not absolute under all conditions is indicated by the fact that I now have two strains of Old-Fashioned Yellow Beans of unknown origin which for several generations have bred true to a distinct runner type of vine. A number of crosses have been made using these runner types of Old-Fashioned Yellow Eye. It is hoped that these and other experiments which have been started will throw some light upon this question.

Attention may be called to the apparent 1:1 ratio of runner to bush in the case of the piebald and Improved Yellow Eye beans. Emerson (1904, 1916), von Tschermak (1904, 1912) and others have shown that in crosses between tall (runner) and dwarf beans the expected F_2

ratio is 3 tall to 1 dwarf. Obviously the present data are of little use in the study of this question because in the first place it consists of a mixture of F_2, F_3 and F_4 plants and in the second place the vine characters of the parents in the different crosses are unknown. · It is quite possible that the parents in the case of pedigree No. 1318 were both of the bush type. The 22 plants in the F_2 generation in this strain are all of the bush type.

The only reason for presenting the data in Table III at this time is to call attention to the relation between the bush type of vine and the Old-Fashioned Yellow Eye pattern. There seems to be no question but that these two characters are closely associated.

LITERATURE CITED

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CHROMOSOME STUDIES ON THE DIPTERA

III. Additional Types of Chromosome Groups in the Drosophilidæ

CHARLES W. METz

Station for Experimental Evolution, Cold Spring Harbor, N. Y.

In connection with other work on the Drosophilas I have for some time been engaged in a comparative study of their chromosomes, with especial reference to possible phylogenetic relationships between different species. A short preliminary report of this study was published two years ago (Metz, '14) after five types of chromosome groups had been found among eleven species. More recently I have studied fifteen additional species of *Drosophila,* one of *Cladochæta* and two of *Scaptomyza* (related genera), and have found several more types of chromosome groups. Altogether twelve main types and several sub-types have been identified—a series more extensive, I believe, than any heretofore recorded among allied species. Of these twelve types all but one are represented in the genus *Drosophila.*

The study has not yet advanced far enough to fulfil the purpose for which it was originally undertaken, but in view of the widespread interest recently attracted to the Drosophilas as objects of genetic research it seems desirable briefly to describe the chromosomes of the species thus far examined without awaiting the completion of the original investigation. In doing this I shall endeavor merely to give an accurate presentation of the chromosomal data, without dwelling on the theoretical considerations they may suggest, considerations which can receive adequate treatment only after many more species have been examined.

Since in almost every case larval or pupal stages are

the only ones suitable for study, it has been necessary to breed the various species in confinement in order to determine their chromosome groups. As a result only about half of those collected have been studied cytologically. Other determinations will be reported in the future as they are obtained.

The material has been secured from four regions, New York, Massachusetts, Alabama and Cuba, with the exception of one species (not found in these localities) from California and Oregon.[1] Fourteen of the twenty-nine species are undescribed and are here given the manuscript names of Dr. A. H. Sturtevant.[2] Descriptions of them are in press.

Most of the chromosome descriptions in the present paper are taken from pedigree material, either first or second generation from wild flies, and the results have been checked up in such a way as to make it very improbable that serious errors have crept in. As mentioned in previous papers the chromosomes of these flies stand out with diagrammatic clearness when favorable figures are secured; and since they are uniformly arranged in pairs and are often of various sizes they offer admirable material for a comparative study. This makes it possible to classify the members of each chromosome group according to their size and shape, and to assort the groups into definite types according to their configuration.

DESCRIPTION OF TYPES

The terminology used in describing the chromosomes will be the same as that used in my previous paper ('14).

[1] The collections, of course, include only a fraction of the existing species within these areas, to say nothing of those in surrounding regions. For more detailed locality references see description of types.

[2] This investigation would have been practically impossible without the cooperation of many friends. In addition to Dr. Sturtevant, to whom I owe all of the identifications, and cultures of several species, I am under obligation to Professor F. S. Earle, Dr. Carlos de la Torre and Mr. C. T. Ramsden for many courtesies shown to me while collecting in Cuba, and to Messrs, L. L. Gardner and G. F. Sykes for Pacific coast material, including *D. obscura.*

Certain recurring kinds will be distinguished in advance and will be designated by name or letter in the specific descriptions.   These are as follows:

V. Long, V-, U-, or dumb-bell shaped chromosomes, attached to the spindle at the median constricted portion (apex of the V).

r. Rod-like, straight chromosomes, approximately half the length of V, attached to the spindle at one end, and radially arranged in metaphase.

c. Short, curved chromosomes, differing from r only in form and (probably) in having a median attachment to the spindle.

m.[3] Minute, spherical or slightly elongate chromosomes, usually located in the center of the metaphase plate.

To these symbols must be added XX and XY, used to designate the sex chromosomes wherever they have been definitely identified.   In some species they are straight, in others V-shaped.   Identification of the sex chromosomes and determination of the XY relations in the males has been one of the most difficult features of the study, owing to the extreme scarcity of spermatogonial and spermatocyte figures; but it has been made in as many cases as possible and has been of great usefulness in comparing different groups.

The order or sequence in which the types are described is a purely arbitrary one, and is not intended to indicate any genetic relationship.

In order to avoid duplication of figures chromosome groups which have previously been described and figured are not reproduced here unless they are of especial interest.   The series of types as a whole may best be understood from an examination of diagrams A to L, which represent schematically, but accurately, the twelve main types.

[3] The term m-chromosome, borrowed from Wilson ('05), is used here in a purely descriptive sense, and is not intended to signify any relationship with the m-chromosomes of the Hemiptera.
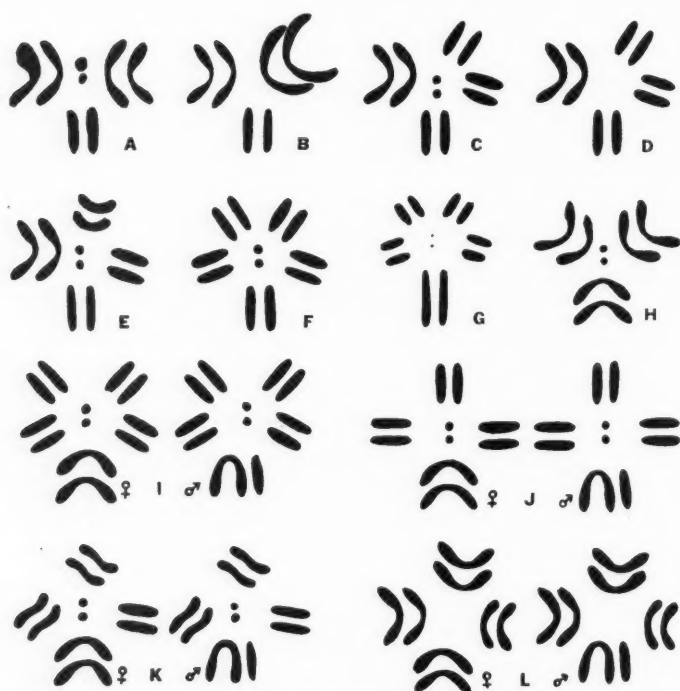
Type A

Represented by

    Drosophila ampelophila Loew. Cosmopolitan.[4]
      (See Stevens, '08, Figs. 57–60, 80–82, Metz, '14,
      Figs. 4 and 5, Bridges, '16, Figs. 1–4, Metz, '16,
      Fig. 19.)

    Drosophila amoena Loew. New York. (Metz, '14,
      Figs. 1–3, Metz, '16, Figs. 13–16.)

    Drosophila busckii Coq. New York. (Metz, '16,
      Figs. 17 and 18.)

    Drosophila bromeliae Sturtevant mss. Cuba.
      (Fig. 1.)

    Drosophila dimidiata Loew. Alabama. (Metz, '16,
      Fig. 20.)

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[4] With the exception of this species, which has been studied by several investigators, localities cited are those in which my cytological material has been obtained.
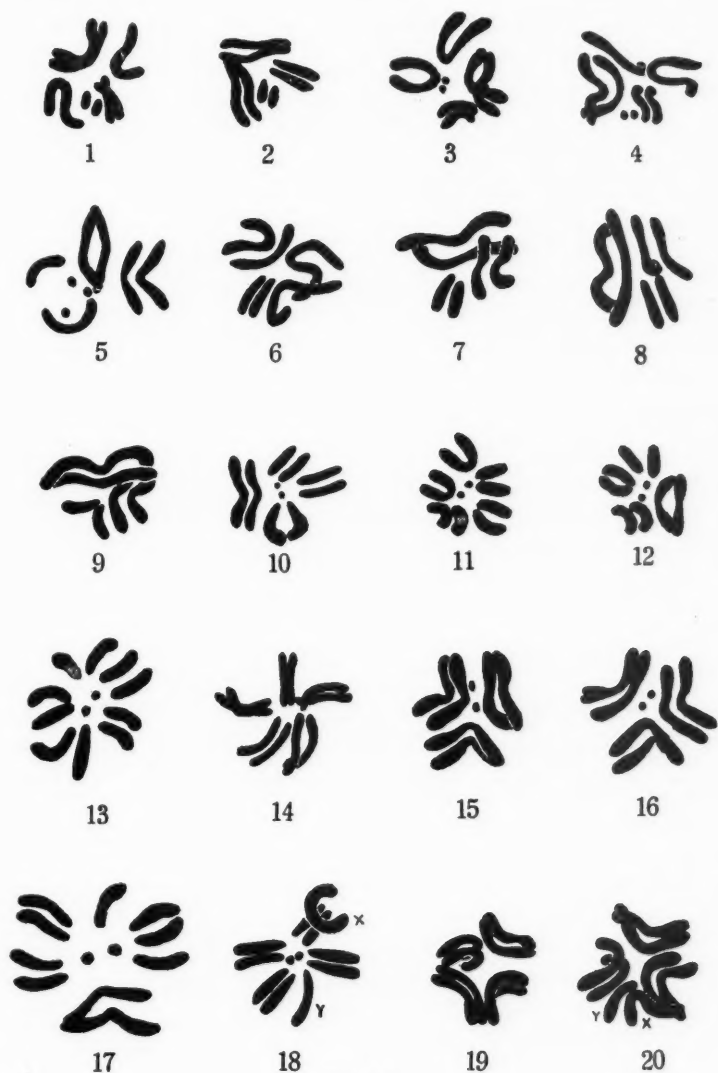
1   2   3   4

5   6   7   8

9   10   11   12

13   14   15   16

17   18   19   20

PLATE I

Explanation of Figures

All figures were drawn with the aid of a camera lucida, using Zeiss 1.5 mm. apochromatic objective and compensating ocular number 12, with tube length of 160 mm. The drawings are reproduced natural size. With the exception of number 17 all are taken from sections cut 5 microns thick.

Drosophila floræ Sturtevant mss.   Cuba.   (Fig. 2.)

Drosophila limbata Will.   Cuba.   (Metz, '16, Figs. 10–12.

Drosophila procnemis Will.   Cuba.   (Metz, '16, Figs. 34–36.)

Drosophila quinaria Loew.   New York.   (Metz, '14, Fig. 7.)

Drosophila robusta Sturtevant mss.   New York. (Figs. 3 and 4; Metz, '16, Figs. 7–9.)

Drosophila saltans Sturtevant mss.   Cuba.

Drosophila pallida Will.   Cuba.

Scaptomyza graminum Fall.   New York.   (Fig. 5; Metz, '16, Figs. 4–6.)

This is type I of my previous paper, and is the prevailing type among the species studied, being represented by thirteen of the total twenty-nine.   It consists of two pairs of long, V-shaped chromosomes, one pair of straight sex chromosomes, and one pair of *m*-chromosomes.

Slight modifications of this type are found in certain species, usually characterized by peculiarities in the sex chromosome pair.   In *D. ampelophila* it appears from the work of Bridges ('16) that the *Y*-chromosome, instead of being straight as is the *X*-chromosome, is hook-shaped or V-shaped, although never large enough to be confused with the V-shaped euchromosomes.   My observations confirm those of Bridges in this regard with the exception of two figures in which *X* and *Y* appear equal and straight.   Perhaps these are due to accident, but they are entire figures and normal in other respects.

FIG. 1.   *Drosophila bromeliæ* Sturtevant mss., spermatogonium.
FIG. 2.   *Drosophila floræ* Stt. mss., ovarian cell.
FIGS. 3 and 4.   *Drosophila robusta* Stt. mss., spermatogonia.
FIG. 5.   *Scaptomyza graminum*, spermatogonium.
FIGS. 6–9.   *Drosophila carlei* Stt. mss., ovarian cells.
FIG. 10.   *Scaptomyza adusta*, ovarian cell.
FIGS. 11 and 12.   *Drosophila neglecta* Stt. mss., ovarian cells.
FIG. 13.   *Drosophila similis*, ovarian cell.
FIG. 14.   *Drosophila cardini* Stt. mss., ovarian cell.   The *m*-chromosomes are not visible in this figure, but are evident in other cells of the same ovary.
FIGS. 15 and 16.   *Cladochæta nebulosa*, ovarian cells.
FIG. 17.   *Drosophila repleta*, variety *b*, ovarian cell.   Taken from an aceto-carmine smear preparation.
FIG. 18.   Same, spermatogonium, from a section.
FIG. 19.   *Drosophila caribea* Stt. mss., ovarian cell.
FIG. 20.   Same, spermatogonium.

In *D. amoena* and *S. graminum* spermatogonial figures indicate that X and Y are unequal and straight (Fig. 5, and Metz, '14, Figs. 2 and 3); while in *D. busckii, D. floræ, D. bromeliæ, D. robusta* and *D. limbata* no inequality is evident. The other species have not been examined with respect to spermatogonial groups. In *D. robusta* the rod-like members (sex chromosomes?) appear to be hook-shaped and to be attached sub-terminally to the spindle in much the same manner as the Y-chromosome in *ampelophila*.

Another modification or sub-type is represented by *D. floræ* and *D. bromeliæ,* in which the *m*-chromosomes are materially larger than in the other species. Indeed, those of the former are so large as to suggest a transition between *m*-chromosomes and *r*-chromosomes.

Type B

Represented by

> *Drosophila earlei* Sturtevant mss. Cuba. (Figs. 6–9.)

This interesting type consists of one short rod-like pair and two large V-shaped pairs, one of which is much longer than the other. No trace of *m*-chromosomes has thus far been found in the fifteen or twenty figures I have studied. Unfortunately I have not yet secured good spermatogonial figures and am unable to identify the sex chromosomes.

In many respects type B is of greater interest than any other type of chromosome group I have studied, for it not only contains the smallest number of chromosomes thus far found among the higher flies,[5] but each of its three pairs is conspicuously different from either of the other two, making possible an individual identification of the chromosomes not obtainable, with such a degree of certainty, in any other known species of *Diptera*. If a genetic continuity of chromosomes be admitted there can be no question that here each paternal chromosome as-

[5] Two species of Culicidæ (*Anopheles punctipennis* and *Culex pipiens*) also have three pairs of chromosomes. See Stevens, '11.

sociates with its corresponding maternal mate.   (See Metz, '16, p. 251.)

Type C

Represented by

>   *Drosophila ornatipennis* Will.   Cuba.   (Metz, '16, Fig. 21.)

>   *Scaptomyza adusta* Loew.   New York.   (Fig. 10; Metz, '16, Fig. 22.)

Type *C* corresponds to type IV of my previous paper ('14), but the single species formerly referred to it has been transferred to type *E*.   Chromosome groups of type *C* are composed of one large V-shaped pair, one long, straight sex chromosome pair, two shorter rod-like pairs and one small *m*-pair.   In both species spermatogonial figures show a noticeable inequality between X and Y; thus identifying the sex chromosomes.

Type D

Represented by

>   *Drosophila tripunctata* Loew.   New York.   (Metz, '14, Figs. 21–26.)

Type *D* corresponds to type V of my previous paper ('14) and includes only one species.   It differs from type *C* in lacking the *m*-chromosome pair, and in sex chromosome relations. X and Y are apparently equal in size and similar to the rod-like euchromosomes.   Their identification is based solely upon their precocious contraction in prophase (see Metz, '14, p. 52), and hence may be held with some reserve, but from analogy with species of types *A* and *C* it seems highly probable that the identification is correct.

Many preparations have been made from material of this species in an attempt to discover an *m*-chromosome pair such as is found in most other species of *Drosophila*, but although stocks have been obtained from several localities and various methods of fixation have been used no trace of the pair has been observed.

Type E

Represented by

> *Drosophila melanica* Sturtevant mss. (two varieties). New York, Alabama. (Figs. 11, 12; Metz, '16, Figs. 23–26.)

The chromosomes of this species resemble those of type *C*, with the exception of one of the short pairs, which is curved or U-shaped instead of straight.   Such a difference in shape is apparently associated with a different mode of attachment to the spindle, and seems to be a characteristic feature.   In my previous paper ('14) *D. melanica* was cited as an example of the type corresponding to *C* of the present paper, and the curved shape of this pair was not considered significant; but more recently I have examined many additional figures and have become convinced that the character is normal and sufficient to distinguish the two types.   The few spermatogonial figures I have examined closely resemble those of female groups and give no evidence of an unequal *XY* pair.

The two varieties[6] of *D. melanica*, although refusing to hybridize, are very similar in external appearance and indistinguishable in chromosomal characters.

Type F

Represented by

> *Drosophila virilis* Sturtevant mss.   New York City. (Metz, '14, Figs. 11–13, Metz, '16, Fig. 2.)
>
> *Drosophila similis* Will.   Cuba.   (Fig. 13.)
>
> *Drosophila ramsdeni* Sturtevant mss.   Cuba.   (Metz, '14, Fig. 10, Metz, '16, Fig. 3.)
>
> *Drosophila cardini* Sturtevant mss.   Cuba.   (Fig. 14.)
>
> *Drosophila modesta* Sturtevant mss.   Alabama.
>
> *Drosophila repleta* Woll., variety *a*.[7]   Cuba, Texas. (Metz, '14, Figs. 8 and 9.)

This type (Type II of the previous paper) differs from *C* in having two pairs of rod-like chromosomes in place of the large V-shaped pair, and from type *A* in possessing

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[6] For discussion of these see forthcoming paper by Dr. A. H. Sturtevant.
[7] See also type *I*.

four rod-like pairs in place of two V-pairs. Next to type *A* this type is of most frequent occurrence, being represented by six of the twenty-nine species.

Spermatogonial figures have been examined in only one of these species, *D. virilis,* and here no conspicuous inequality between X and Y is to be seen. One pair of chromosomes appears to be larger in nearly all figures of either sex, and a slight difference in length between the two members of this pair may be seen in some male figures, but it may be purely accidental.

Type G

Represented by

    Drosophila funebris Fabr. New York, California, North Dakota. (Metz, '14, Figs. 14–17,[8] Metz. '16, Figs. 27–33.)

This interesting type (type III of the previous paper) is apparently a modification of type *F,* but differs from it in the relative proportions of all of the chromosomes. The *m*-chromosomes are so minute in most specimens as scarcely to be visible, and for this reason were entirely overlooked at first. Their conspicuousness doubtless varies with the amount and kind of stain, and with the fixative used, but even after making full allowance for this there can be no doubt that the pair is much smaller here than in most other species. Otherwise the type is characterized by the smaller size of the short, rod-like chromosomes and the greater length of the longest (sex chromosome?) pair. As in the preceding case no conspicuously unequal XY pair is to be found in the males, although a noticeable difference between the two large chromosomes may be seen in some of the figures.

Type H

Represented by

    Cladochaeta nebulosa Coq. Cuba. (Figs. 15 and 16.)

This species—the only known member of the genus—is

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[8] Fig. 14 (Metz, '14) and Fig. 27 (Metz, '16) are from the same cell; the latter drawn after the *m*-chromosomes were discovered.

included in the present review because of its obvious rela-
tionship to the true Drosophilas.   The type of chromo-
some group which it represents is the only one of the
twelve not thus far found in some species of *Drosophila*,
and its general similarity to some of the *Drosophila* types
is marked.   Female groups consist of three similar pairs
of long, V-shaped chromosomes and one small pair of
m-chromosomes.   Unfortunately the species breeds very
poorly in confinement and no male preparations were
secured.   It is almost certain, however, that one of the
long pairs is the sex chromosome pair.

Type I

Represented by
> *Drosophila repleta* Woll., variety *b*.   New York,
> Massachusetts, California.   (Figs. 17 and 18;
> Metz, '16, Figs. 39–41.)

In my 1914 paper *D. repleta* was referred to the type
corresponding to *F* of the present study, but it is now
evident that two very similar but distinct varieties of the
species occur, characterized, among other things, by de-
cidedly different sex chromosomes.   In one, the sex
chromosomes are short and rod-like in the female and
presumably so in the male, while in the other they are
long and V-shaped in the female and markedly unequal in
the male.   The latter represents the present type *I*.   The
difference between the two may be readily appreciated
by an examination of diagrams *F* and *I*.   Although it
relates only to the sex chromosomes it is very striking in
the females, and easily separates the two varieties into
distinct types.   The fact that the two forms can not be
induced to hybridize lends support to the chromosomal
evidence of their distinctness, but externally they are
astonishingly similar and are referred to the same species
by Sturtevant.[9]

[9] It may be noted that these are not the "light and dark" varieties de-
scribed by Sturtevant ('15), both of which belong to type I.

Type J

Represented by

Drosophila obscura Fall. California and Oregon.
(Metz, '16, Figs. 44–50.)

Ovarian cells of *D. obscura* contain three rod-like eu-chromosome pairs, one small *m*-chromosome pair and one very long, V-shaped sex chromosome pair (diagram *J, ♀*). In the male the sex chromosomes are very dissimilar, *Y* being straight and only about half as long as *X*.

Type K

Represented by

Drosophila affinis Sturtevant mss. Alabama.
(Metz, '16, Figs. 42 and 43.)

In general this type resembles the last, but differs in having two S-, or hook-shaped pairs in place of rod-like ones. Apparently this peculiar shape is due to a sub-terminal attachment to the spindle, although I have been unable to get figures actually demonstrating the attachment. In some cases one or both pairs extend radially from the center of the figure as if they were attached terminally, but usually their position is characteristically that described above. In any event the two pairs are readily distinguished from any others of the group, unlike those of *D. obscura*.

Type L

Represented by

Drosophila caribea Sturtevant mss. Cuba, Panama.
(Figs. 19 and 20.)

This type is radically different from any of those described above, and like the two preceding is represented by only one species. Female (ovarian) groups are composed of four long V-shaped pairs of chromosomes, one, of which is shorter than the other three. In the male one pair is conspicuously unequal, much as in types *I, J* and *K*, but I have been unable to determine with certainty whether this is the small pair or one of the large ones. It is represented as a large one in the diagram (*L, ♂*).

Several of the species contained in this survey have been, or are being used in genetical studies. With the exception of the well-known *D. ampelophila* these are included in the following list, together with references to literature dealing with them, so far as known to me:

D. repleta, type *H.,* Sturtevant, '15, Hyde, '15.

D. affinis, type *J.* Hyde, '15.

D. tripunctata, type *D.*   Metz and Metz, '15.

D. virilis, type *F.*   Metz and Metz, '15.

D. similis, type *F.*   In press.

D. obscura, type *I.*   In press.

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THE SHAPE OF THE STERNUM IN SCORPIONS AS A SYSTEMATIC AND A PHYLOGENETIC CHARACTER

ALEXANDER PETRUNKEVITCH, Ph.D.,

ASSISTANT PROFESSOR OF ZOOLOGY IN THE SHEFFIELD SCIENTIFIC SCHOOL

(From the Osborn Zoological Laboratory of Yale University)

IT is generally recognized that the shape of the sternum furnishes one of the important characters for the distinction of families in recent scorpions. The small family Bothriuridæ is the only one in which the sternum is composed of two transverse plates. This family includes seven genera, six of which occur in South America, while the seventh (*Cereophonius*) is an inhabitant of South Australia and contains a single species. The families Scorpionidæ, Vejovidæ, Chærilidæ and Chactidæ have a distinctly "pentagonal" sternum with more or less parallel sides. The Chærilidæ belong exclusively to the old world. The Chactidæ are divided into three subfamilies, the European Euscorpiinæ and the neotropical Megacorminæ and Chactinæ, which have Mexico for their northern limit of distribution. The Vejovidæ are unevenly distributed between the Old World and the New. One of the eight genera composing this family is found on the shores of the Mediterranean (*Iurus,* with a single species *I. dufoureius*), another (*Scorpiops*) with about eight species in East India. Of the remaining six genera, two occur in South America, while the other four belong to the southern and western United States and to Mexico. The family Scorpionidæ, to which some of the largest scorpions belong, has representatives from various countries and regions. It is usually divided into five subfamilies. Of these the Urodacinæ are Australian; the Scorpioninæ Asiatic and African; the Hemiscorpioninæ Asiatic; the

Ischnurinæ African, Asiatic and neotropical (*Opistha-canthus elatus* is the single neotropical species); the Dip-locentrinæ neotropical and Asiatic (a single genus with two species from eastern Asia).

All scorpions belonging to the large family Buthidæ have a distinctly "triangular" sternum with converging sides and truncated apex. The family is naturally divided into two large subfamilies. Of these the Buthinæ may be regarded as belonging to the Old World, since of its 14 genera a single genus and species (*Ananteris balzani*) is found in South America. The subfamily Centrurinæ includes four genera. The genus *Isometrus* is characteristic of the Old World but its commonest species, *I. maculatus,* is cosmopolitan and occurs in Florida, Hawaiian Islands, South America, etc. *Zabius* is South American. *Titius* is neotropical, although one species, *T. floridanus,* occurs in southern Florida. The largest genus, *Centrurus,* is represented by some of the commonest species in the southern United States and the subtropical and tropical America.

Let us fix our attention for a moment on the distribution and characters of two genera of scorpions common to the United States. One is *Vejovis* (of the family Vejovidæ) and is represented in this country by six species; the other is *Centrurus* (of the family Buthidæ) and is represented by seven species. *Vejovis* belongs more to the southwest and west. It is distributed through California, Nevada, Utah, Arizona, New Mexico and Texas and extending northward into Idaho and Nebraska. A single species, *V. carolinus,* is found in the southeast. It occurs as far north as South Carolina and spreads southward to the Gulf states and Texas. Except possibly this species, the other species of *Vejovis* occur also in Mexico where the genus is represented by four additional species which do not occur in the United States. I have besides, in my private collection, a new species of *Vejovis* from Terra del Fuego. *Centrurus* belongs more to the southeast. A single species (*C. exilicauda*) occurs in

California.   *C. nigrescens,* a variety of the more south-
ern *C. gracilis,* has been reported from Texas.   Four
species occur in Florida, but of these *C. gracilis* and *C.
margaritatus* belong to a more southern fauna, the latter
being the most common scorpion of Mexico and Central
America.   One species, *C. infamatus,* has practically the
same distribution as *Vejovis carolinus,* spreading north-
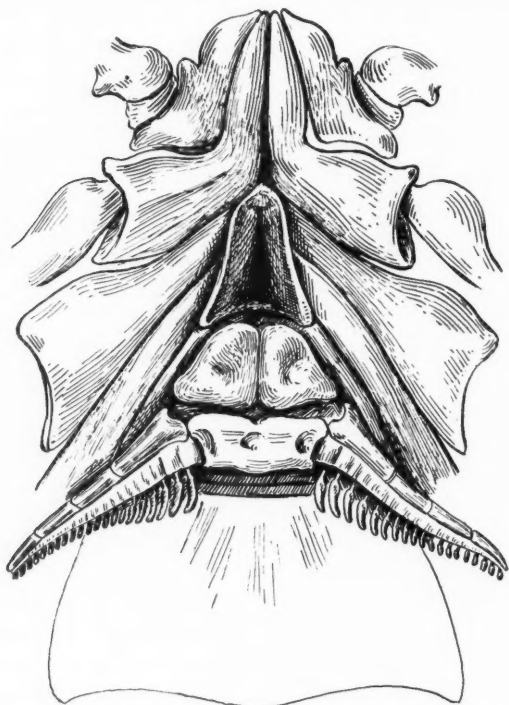ward into South Carolina and southward into Texas and

Fig. 1.   Sternum, genital opercula, combs and coxæ of an adult *Centrurus
insulanus* Thorell from Jamaica, W. I.   The sternum is "triangular" with con
verging sides, but still shows traces of its original, pentagonal shape.

northern Mexico.   *C. infamatus* is the common scorpion
of the southeast and south.   Several other species of *Cen-
trurus* are characteristic of tropical North and South
America.

Vejovis carolinus is a small scorpion, its length not exceeding 34 mm. The width of the carapace at the posterior edge is slightly less than the length. The center of the eye tubercle is about $\frac{2}{3}$ of the entire length of the carapace from its anterior edge. The sternum is pentagonal; the comb has 13–14 teeth; the central and inner rows of plates in the comb are beadlike. The fingers are rather short, being either as long as or only slightly longer than the hand.

Centrurus infamatus is usually about 45 mm. long, but large specimens measure up to 70 mm. The width of the carapace at the posterior edge is equal to or even slightly exceeds its length. The center of the eye tubercle is about $\frac{2}{3}$ of the entire length of the carapace from its anterior edge. The sternum is triangular. The comb usually has 18–19 teeth, although their number may reach 25. The central rows of plates is not beadlike, but composed of five plates the limits between which are difficult to ascertain. The inner row is beadlike. The fingers are rather long, being more than $1\frac{1}{2}$ times as long as the hand.

Let us now consider the Palæozoic scorpions. The sternum of the Silurian *Proscorpius osborni* Whitfield is unfortunately not preserved. Its nearest European relative, the Silurian scorpion *Palæophonus hunteri* Peach, has, according to Pocock, a pentagonal sternum. The sternum of the carboniferous scorpions is fairly well preserved in many specimens. The family Isobuthidæ differs from all other fossil and recent scorpions in the position of the fourth pair of coxæ which abut against the genital opercula. The sternum is either triangular (*Palæobuthus*), rhomboidal (*Isobuthus*) or oval (*Eobuthus*). The family Cyclophthalmidæ has a "pear"-shaped sternum, the family Eoscorpionidæ a distinctly pentagonal one with parallel sides. If the pear-shaped and rhomboidal impressions of sterna do not owe their shape to poor preservation or displacements, then these types of sterna must have disappeared completely, as has the type of triangular sternum found in Isobuthidæ. Of

preserved fossils there remain then only the Silurian
Palæophonidæ and the carboniferous Eoscorpionidæ hav-
ing a sternum and arrangement of coxæ similar to that
in recent scorpions. But the Silurian scorpions pos-
sessed other characters of their own and have either dis-
appeared completely or perhaps have changed gradually
into carboniferous forms. In the absence of Mesozoic
fossils any attempt to trace relationships between recent
and Palæozoic scorpions can be only conjectural. Thus
in my ''Monograph of Palæozoic Arachnida'' I arrived
at the conclusion (p. 26) that '' the family Eoscorpion-
idæ shows many relations to the recent Scorpionidæ and
Vejovidæ and represents probably two or three families
thrown together for lack of distinctive characters.''   In
formulating this opinion I was guided chiefly by the shape
of the sternum, in several cases remarkably well pre-
served. Since that time I have made an observation, in-
significant in itself, but one which affords an insight into
the past history of recent scorpions possessing a trian-
gular sternum and suggests a closer relationship between
the Eoscorpionidæ and the Centrurinæ than between the
former and the Vejovidæ. This observation was made
by pure chance. While studying the problem of seg-
mentation in Arthropods, I was examining a frontal sec-
tion through a recently born *Centrurus insulanus* from
Jamaica (Fig. 2). To my amazement the sternum proved
to be beautifully pentagonal. An error of identification
was excluded. I myself collected the material and pre-
served the adult females with the young carried on their
back. Yet if objection should be raised, a final proof is
offered by the fact that late embryos, too, have a pentag-
onal sternum and such embryos are easily obtainable
from adult, gravid females. (Scorpions are without ex-
ception viviparous.)   The young of *Centrurus infamatus*
also have a pentagonal sternum, as have probably the
young of all other species of the genus *Centrurus*. It is
strange that no one has noticed this before, since there
must be dozens of specimens in every museum. I find

an interesting confirmation of my observation in Fig. 10
of McClendon's paper on the nervous system of *Cen-
trurus infamatus*.[1]   The adults of his material were iden-
tified for him by no less an authority than Kraepelin, yet
in the figure in question McClendon draws a distinctly
pentagonal sternum in a surface view of a late embryo.
The case is the more interesting because McClendon him-
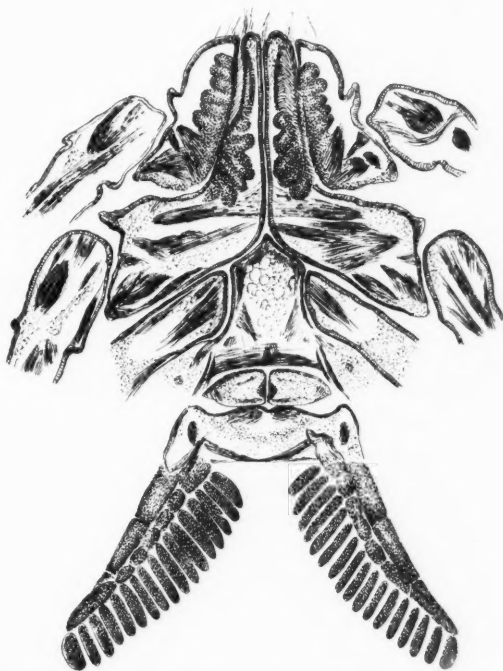self is unaware of the value of his observation, nor is

FIG. 2.   Frontal section parallel to the ventral surface showing sternum,
genital opercula, combs and coxæ in a very young *Centrurus insulanus*.   The
sternum is distinctly pentagonal, with parallel sides.

there the slightest reference to it in the text.   He simply
drew the sternum as he saw it, without so much as men-
tioning it.   An examination of the adults of *Centrurus
insulanus* (Fig. 1) as well as of other species of *Cen-*

[1] *Biol. Bull.*, Vol. 8, 1904, p. 51.

trurus, shows that their sternum retains throughout life traces of its origin from a pentagonal prototype. Only the triangular apex is comparatively small and more or less hidden between the coxæ, and the sides of the sternum are strongly convergent, not parallel. The sternum in adults of various species of Buthinæ of the Old World shows also a small triangular apex hidden between the
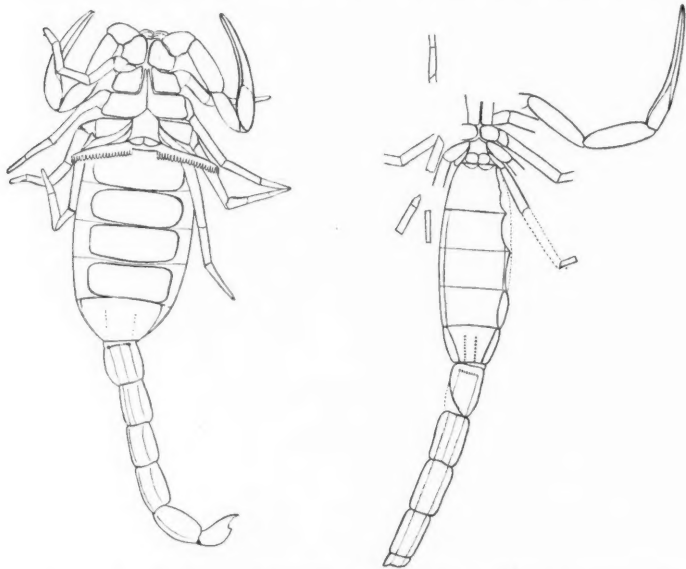

FIG. 3. A very young *Centrurus infamatus* (C. l. Koch) = (*carolinianus* Palisot de Beauvais) drawn with the aid of the Abbe apparatus. The sternum is pentagonal. The hand has much longer fingers than would be the case in an adult of the same species. Abdomen distended by yolk.

FIG. 4. *Eoscorpius typicus* Petrunkevitch, from Mason Creek, Illinois. Specimen No. 37986 of the U. S. N. M. (Fig. 6 of the Monograph.)

coxæ, and in the absence of material I venture the prediction that the embryos will be proved to possess a pentagonal sternum.

Keeping this in view, let us now compare *Centrurus infamatus* with *Eoscorpius typicus* of the Pennsylvanic from Mason Creek, Illinois, a rather well-preserved Palæozoic scorpion of approximately the same size. Fig. 4

is taken from my monograph and represents the holotype of *Eoscorpius typicus* as it appears on the reverse.   Fig. 3 is a careful drawing of a very young *Centrurus infamatus* made with the aid of an Abbe apparatus.   This figure is much more enlarged than is Fig. 4, to facilitate comparison.   The shape of the abdomen, as is well known, is the least constant character and we will leave it out of consideration.   To avoid criticism, however, I would state that the great distension of the abdomen in the young *Centrurus* is due to the presence of embryonic yolk. When this disappears, the abdomen becomes much thinner.   In older specimens the distension of the abdomen is frequently due to the growing embryos.   Yet, in dissecting what I supposed to be gravid females, I was surprised to find no embryos in them and only small ovaries. The fact is that the distension of the abdomen is also often due to the condition of the liver.

The carapace has a fairly constant shape and is similar in both scorpions.   For figure and measurements I refer to my monograph.   I do not reproduce them here because the carapace of *Vejovis,* except for its size, is also of similar shape.   The rows of granules on the caudal segments are not sufficiently well preserved in the fossil specimens to allow of a conclusion as to their exact number.   On the other hand, the transverse row of granules at the anterior end of the first caudal segment, present in *Eoscorpius* and wanting in the adult *Centrurus,* is clearly defined in the young.   The most interesting character is represented in the hand with its fingers.   As a rule the ratio between the length of the fingers and that of the hand is a fairly constant one for each species.   In the holotype of *Eoscorpius typicus* it is approximately $2:1$; in the adult *Centrurus infamatus* it is $1.6:1$, but in the late embryos and just born young it also approximates $2:1$.   With other words, *Centrurus* developed from an ancestor with relatively longer fingers and the trend of evolution was toward reduction in their length.

One character presents a difficulty.   This is the comb.

Specimen No. 37987 of the U. S. Nat. Mus. of *Eoscorpius* shows a comb which is very broad at the base, and has, apparently, a single median plate, a beadlike inner row and 19 teeth. I identified this specimen as *Eoscorpius typicus* for the reason that "the general appearance of the specimen, the shape "of the tergites, especially of the seventh," strongly resembled the holotype. The specimen is incomplete and about twice as large as the holotype. Perhaps No. 37987 is after all of a different species. The shape of the comb in recent species of *Centrurus* is not always the same as in *infamatus*. The comb in *C. junceus* and *C. agamemnon* is twice as wide at the base as in the middle.

Taking all characters and the geographic distribution into account, we can not fail to notice the greater similarity between the young of *Centrurus infamatus* and *Eoscorpius typicus* than between the latter species and *Vejovis*. What advantage, if any, *Centrurus* has derived from the shortening of the fingers and the change in the shape of the sternum, is a totally different question which may possibly be answered by studying the functions and uses of these organs in recent species.

THEORIES OF HIBERNATION

ANDREW T. RASMUSSEN

CORNELL UNIVERSITY

An examination of the literature on almost any particular natural phenomenon often reveals the fact that many different theories have been advanced to explain it. Some of these explanations may be mere opinions based upon no or but few scientific facts. One is also frequently struck with the immense literature that has been produced and the great gap that still intervenes between the accumulated facts and a clear understanding of the processes which they aim to elucidate, even after more than a hundred years of experimental work, which has usually been preceded by a much longer period of speculation by the great thinkers of the past. So that while we congratulate the last few generations upon the rapid growth that has been made in scientific knowledge, there yet remain phenomena that are almost as unintelligible to-day as they were a hundred years ago—the most earnest and often tedious experimentation and observations of several generations having shed but little light on the factors and mechanism involved.

The extremely interesting fact of hibernation (called "*Winterschlaf*" by the Germans, "*sommeil hivernal*" by the French and "*letargo*" by the Italians) illustrates well the above point. As is well known, during this dormant state the vital processes are greatly reduced. The changes that occur are especially marked in certain mammals, since they apparently undergo a rather sudden transformation from the warm-blooded (homoiothermal) type to the cold-blooded (poikilothermal) type. In the latter state such mammals are able to endure cold, deprivation of food, confined air, effects of many drugs, and other conditions that would be fatal at other times. Naturally

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such profound physiological changes, in some respects almost as striking as the latent vitality of the seeds of plants and the spores of lower organisms, has aroused the attention of a great many observers. In fact, the literature on hibernation dates back to the time of Aristotle (384–322 B.C.), though real experimental work for the purpose of understanding the nature and cause of this torpid state, commenced with Conrad Gessner[1] (1551). From that date to the present there has accumulated a vast amount of data, the bibliography of which is now very accessible, due to the extensive works of Raphael Dubois,[2] published in 1896, and of Osvaldo Polimanti,[3] published in 1912.

As the exciting cause of so-called winter-sleep, cold has naturally received by far the greatest share of attention. A rapid survey of the subject shows that much difference of opinion has existed in regard to the manner in which cold acts and what other factors are involved. Buffon[4] (1749) and Lacépède[5] (1829) thought that the blood simply becomes cold when the small amount of heat produced by hibernating animals is not aided by the surrounding temperature. The cold blood then produces the changes characteristic of torpidity. Spallanzani[6] (1787), however, considered that he had experimentally demonstrated that the cold acts on the solid tissues of the body and not on the blood. According to him the lethargy is due either to the stiffening of the muscles or to the depletion of the cerebral blood vessels. On the other hand, Alibert[7] maintained that the cold diverts the blood from the periphery to the vessels of the brain and the resulting congestion causes torpor. But Serbelloni[8] (1866) claims to have found the vessels of the brain nearly empty in the case of three marmots in full hibernation. Hunter[9] (1775) and Serbelloni explained that the cold causes the animal to lose its appetite and in the absence of hunger, which is a stimulus, the animal retires.

A long list of authors, Daubenton[10] (1760), Geoffroy,[11] Cleghorn,[12] Allemand,[13] Carlisle[14] (1805), Barkow[15]

(1846) and others, have emphasized also the necessity of confined air or diminished respiration, Cleghorn and Allemand maintaining that this is the principal cause. Reeve[16] (1809) said that such a condition favors winter-sleep, while Bert[17] (1868) first concluded that lack of oxygen and then later[18] (1873) that the accumulation of CO_2 in the surrounding air might be the cause of dormancy. Mangili[19] (1807), however, denied that vitiated air has anything to do with this torpid state and Dubois[20] (1896) says that confined air is not necessary, for animals hibernate perfectly in well-ventilated places.

Marshall Hall[21] (1832) believed that the cold caused ordinary sleep, which diminishes respiration, and less heat is produced. Lessened respiration causes the blood to lose its arterial character and hence its power to stimulate the heart. The heart, however, changes its irritability so that it does not stop. This change in the irritability of the heart, then, is the important factor in hibernation. To him winter-sleep is something entirely different from the torpor produced by cold. To Edwards[22] (1824) and Legallois[23] (1824) sleep and cold are so bound up with heat production that a failure to keep up the body temperature causes torpidity to ensue.

Throughout the literature of the last one hundred years there is a strong tendency to consider hibernation as differing from ordinary daily sleep only in degree. Edwards[22] (1824), Dugé[24] (1838), Hall[21] (1832), Blandet[25] (1864), Patrizi[26] (1894), Dubois[27] (1896, 1910), Brunelli[28] (1902), Claparède[29] (1905), Allen Cleghorn[30] (1910) and Salmon[31] (1910) make definite statements regarding the striking similarity between ordinary daily sleep and hibernation. Gemelli[32] (1906) used the facts obtained by him from hibernating marmots, in disproving Salmon's theory of sleep. Indeed, it has been the hope of many of the students of hibernation to be able to throw some light on the process of diurnal sleep in man and other animals, by a study of what they have considered to be merely an extreme example of this physiological condition. The

discussions on sleep that appeared in the *British Medical Journal* in 1913 and the comprehensive treatise by Pieron[33] (1913) on the physiological problem of sleep, clearly indicate how little has been accomplished in this direction. Buffon[4] (1749), on the other hand, thought that ordinary sleep and hibernation were something entirely different. Monti[34] (1905) even now believes that these two forms of sleep have entirely different physiological meanings and that hibernation in its phylogenetic study should be compared with the dormancy of lower forms, as well as with ordinary sleep.

In reply to the question asked by the French Academy of Science over a hundred years ago as to the cause of this lethargy and why it pertains to certain animals, Saissy[35] (1808) stated that the cause fundamentally is to be found in certain anatomical peculiarities such as the enlarged character of the heart, central blood vessels, thorax, abdomen and cutaneous nerves, and the smallness of the peripheral vessels and lungs. To these he also added as important features the liquid quality of the blood and the sweetness of the bile. The diversion of the blood from the surface towards the center of the body, as a result of the external cold, dilates the heart and blood vessels of the thorax, and this interferes with respiration, thus decreasing heat production. As a consequence the animal becomes cold and numb. Prunelle[36] (1811), Barkow[15] (1846), Serbelloni[8] (1866) and Blandet[25] (1864) similarly believed in the importance of such—largely imaginary—morphological features.

Many investigators have associated hibernation with the nervous system. Claude Bernard[37] (1855–76) thought that the cold acts on an unusually well developed peripheral nervous system, and by slowing respiration cools the body. This is a loss of stimulus to the heart and muscles and torpor results. Reeve[16] (1809) stated that cold acts on a special organization of the nervous system, which causes diminished respiration, etc.; while Quincke[38] (1882) interprets the facts he and others have observed,

in connection with the marmot, as indicating the existence
of a heat center in the brain through whose influence on
the various organs of the body, metabolism and heat regu-
lation are so affected as to produce winter-sleep.   The
altered respiration and circulation are secondary results.
Dutto[39] (1896) is also inclined to believe that hibernation
strictly depends upon the regulative influence of the nerv-
ous system upon metabolism and thermogenesis.   He
further considers that the marmot has the power to emit
more heat than has the rabbit, so that torpor may be
based upon the difference in the power of the integuments
of hibernating and non-hibernating animals to lose heat.
Merzbacher[40] (1904), after reviewing much of the liter-
ature dealing particularly with the rôle of the external
temperature, food and the nervous system in the produc-
tion of winter-sleep, concludes that the external cold is
only a secondary aid.   Cold, like abstinence from food,
immobility, slower respiration and lack of oxygen, simply
makes it easier for the animal to cool off and remain cold,
and tends to make the sleep more profound.   The essen-
tial characteristic of the hibernating animal, as compared
with the non-hibernating animal, according to him, is its
ability to change at a rather definite period and in a com-
paratively short time from the homoiothermal to the
poikilothermal type and again at the end of hibernation
to return rather abruptly to the former condition.   The
explanation of both of these alterations, he thinks, is prob-
ably to be found in a certain nervous mechanism in the
mid-brain and medulla which is capable of influencing res-
piration, circulation and metabolism, and, in short, the
production and loss of heat.   The other changes charac-
teristic of the lethargy are natural consequences of and
adaptations to the hypothermic and hypofunctional con-
dition.

In addition to other internal factors there is, accord-
ing to Barkow[15] (1846), a special susceptibility to the ex-
ternal cold due to a rather primitive organization of hi-
bernating animals.   Noè[41] (1903) thinks that a primitive

structure of the organism is the important cause of the
lethargy; but it acts as a mechanism of economy by in-
creasing the resistance of the animal to cold, rather than
to starvation, and thus prevents histolysis from reaching
a dangerous point. An inefficient heat-regulating mech-
anism has been considered the true explanation of winter-
sleep by such men as Dugès[24] (1838), Marès[42] (1889), and
Polimanti[43] (1904). Simpson[44] (1911) in this laboratory
has shown that the woodchuck can not be said to ever
have a normal temperature in the sense that a homoio-
thermal animal has. Merzbacher[40] (1904) cites many
cases similarly indicating the weak thermogenic organi-
zation among winter-sleepers. Recently Polimanti[45]
(1914) has explained his views concerning this labile
thermogenic organization. To him it is due to the fact
that at some remote period all animals then existing
periodically fell into lethargy. With evolutionary de-
velopment most mammals and all birds lost this ability.
Hibernating animals, however, are still able to return to
this cold-blooded type when the heat-producing reflexes
fail, which they are apt to do when the cold becomes ex-
treme. Marès[46] (1913) holds fundamentally this same
view—a view he advanced in 1889. He says that the
cause of hibernation is in the organism itself. He re-
gards the facts presented by Pembrey[47] and Babák[48] and
others concerning the poor heat-regulating mechanism of
the newborn in man and other animals, as well as those by
Merzbacher[49] on the return of the nervous system to a
more segmental type during winter-sleep, as strong evi-
dence in favor of the theory, and as indicating that hiber-
nating animals merely revert to a more primitive type in
which there is no specific sensibility to the outer cold, *i. e.*,
in which no specific heat-regulating reflexes are called
forth by the external temperature. He further thinks
that since the weakness is in the nervous system, it ought
to be possible to bring about some of the conditions of
torpor by means of hypnotic suggestions. He and Hel-
lich[50] (1889) succeeded by this means in getting a fall of

2.5° C. in the body temperature of a hysterical woman. Others have gone much farther in this regard. Thus Liébeault[51] (1866) and Forel[59] (1877), especially the latter, consider hibernation similar in nature to hypnotic sleep. To Marès, however, the initial cause of winter-sleep is the ability of the nervous system to loose its specific sensitiveness to the external cold. This sensitiveness, he thinks, does not belong to the fundamental properties of the nervous system, since it is not found in the young undeveloped animal. It is a property acquired slowly ontogenetically just as it was slowly acquired phylogenetically by the two highest classes of animals. A similarity between the hibernating and fetal states was noted long ago by Pallas[53] (1778), Prunelle[36] (1811), Tiedermann[54] (1815) and Edwards[22] (1824). Tiedermann claimed that in both states there is merely a vegetative existence, hardly any appreciable difference between the appearance of the venous and arterial blood, much serum and little clot when the blood coagulates, a low body temperature, an enlarged thymus (he included the hibernating gland as part of the thymus) containing a fluid, and a secretion of bile. He therefore considered winter-sleep as a periodic return to a fetal state. Pembrey and Hale White[55] (1896) regard the evolution of hibernation, not as the acquisition of a new power, but as a retention of one already present, as is evident from the condition of young mammals and birds in whom the heat-regulating power is inefficient.

Many observers have questioned the value of cold as a factor in the production of this dormant state. Quincke[38] (1882) thought that rest and an appropriate temperature generally, though not always, cause torpor, and yet he said that there seems to be some relationship between degrees of lethargy and external temperature. Blandet[25] (1864) considered that winter was only occasionally, if at all, the cause; while Horvath[56] (1872–81), with whom Bunge[57] (1901) seems to agree, said that hibernation is not sleep at all and that winter has nothing to do with it.

Hahn[58] (1914) concludes that the torpid condition is not
dependent upon cold weather, although his thirteen-lined
ground squirrel usually hibernated with each cold spell
and woke up with the return of warm weather. Experi-
mentally it was early shown that cold will not induce
typical lethargy. Thus Buffon[4] (1749) in the case of the
hedgehog, Daubenton[59] in the hamster, Hunter[9] (1775)
in the dormouse, Mangili[19] (1807) and Bossi[6e] in the mar-
mot, Horvath[56] in the spermophile and hedgehog and
Marès[42] (1892) in the spermophile, have failed to induce
true hibernation by exposure of the animal to low temper-
atures. Saissy[35] (1808) is supposed to have produced
winter-sleep by continued cold and confined air; but like
some other reported cases of artificially produced torpor,
it is not clear that the experimentally produced state was
the same as true hibernation. Sacc[61] (1858) after eight
years of observation on the marmot could see no relation-
ship between the condition of the atmosphere and winter-
sleep. Mills[62] (1892) found that while bats could be
worked like a machine by varying the temperature, mar-
mots, on the contrary, showed a surprising indifference
to the surrounding temperature. Berthold[63] (1837)
claims that dormice became dormant in a room kept warm
(16° C.) all winter, though torpidity was delayed two
months. Merzbacher[4e.] (1904) mentions similar experi-
ences of his own with a bat, as well as several other com-
parable cases. Mangili[19] (1818) saw a dormouse fall into
lethargy in the month of June and not wake up till the
middle of July. Forel[52] (1887) records that two dormice
which remained awake and active all winter, became tor-
pid in May and remained in this condition till August in
spite of the great heat. Marès[42] (1892) found that some
spermophiles and hamsters may hibernate in September
at 16° C. while others remain awake all winter although
the thermometer falls below zero. Hence he concluded
that cold does not cause winter-sleep. Valentine[64] (1857),
Horvath[56] (1881) and Quincke[38] (1882) have observed
marmots become dormant during the summer. Hence

Pembrey[65] (1898), while recognizing that want of food and cold seem to be the most important factors in hibernation, says that some other condition yet unknown is necessary to explain such lethargy during the summer.

As a result of the uncertain action of cold, certain other external conditions have been considered the real exciting cause of hibernation. The food factor was emphasized by Mangili[19] (1807), who believed that neither cold nor vitiated air has anything to do with the production of this torpid state. He thought fasting was necessary because, of several animals under the same external conditions, those animals that were fed did not become dormant, while the non-fed ones did. Marshall Hall[21] (1832) stated that the lack of food predisposes the animal to torpor by rendering it more susceptible to cold. Sacc[61] (1858) concluded that, while he could see no relationship between the atmosphere and torpidity, he could see some connection between the fatness of the animal and the length and profoundness of winter-sleep. He, therefore, concluded that obesity, in connection with fatigue, is the cause of hibernation. Claparède[29] (1905) and Forel[52] (1887) think that the amount of fat may be an important factor, while Beretta[66] (1902) opposes this idea. Simpson[67] (1912) finds that feeding woodchucks greatly interferes with winter-sleep, at least in captivity. Albini[68] (1901) in case of the marmot, and Reeve[16] (1809) in connection with dormice and hedgehogs, also confirm the observation of Mangili on the rôle of food in preventing hibernation. Yet it appears that these animals (marmots) may go into winter sleep while plenty of food is available. Thus Mills[62] (1892) found that during the winter of 1890–91 a marmot hibernated in a cage provided at all times with plenty of food; but during the two following winters two other marmots, kept in the same room and in the same cage under similar conditions, did not hibernate at all, though the temperature got low enough to freeze the water in the cage. It is also a common observation that some of these animals naturally retire

while food is plentiful. Allen Cleghorn[30] (1910) questions the lack of food as a factor in producing lethargy because spermophiles and marmots hide away for winter when their food supply is at its best. In British Columbia he finds that these animals retire a month earlier in the lowland than at the timber line because, he thinks, in the latter region they have not had time to acquire enough fat, since at the timber line they come out of hibernation later in the spring. Thus it is not clear exactly what part food plays in the production of this dormant state.

Treviranus[69] (1802) said that the cause of torpidity during winter lies in the ability to live with all the vital processes at a minimum. This is an acquired character resulting from the habit of sleeping during winter, as is evident, he thought, from the fact that it is lost in marmots kept in captivity. The earlier opinion of Barton[70] (1799) was that it is an accidental circumstance and not a specific character. The general idea, however, that some sort of instinct, in connection with other factors, is involved, was held by Reeve[16] (1803), Barkow[15] (1846), Claparède[29] (1905) and others. Desjardine[71] (1843) thought that the need for sleep in rodents is as great as the necessity of migration in birds. Blandet[25] (1864) described winter-sleep as a relic—an echo from remote periods when this phenomenon was general, having developed as a result of winters so severe that unless this conserving process was resorted to, the animals would have perished. Hibernation is thus, according to this author, the effect of habit and annual periodicity. It still persists in certain animals, but will soon become extinct. Brunelli[28] (1902) believes that this tendency is the result of a long period of evolution favored by the nature of the burrow, etc., where hibernation takes place. But according to Albini[68] (1894) the factors aiding this evolution are not remoteness or other conditions of the burrow, but the immobility of the animal. Carlier[72] more recently (1911) classifies hibernation with estivation (summer-sleep) and migration. Winter-sleep in mammals like the instinct

of migration in birds, he thinks, may have developed in remote ages, the prime cause being want of food, and not cold.

Dubois[73] (1895) has developed a *carbonic auto-narcosis* theory according to which hibernation is due to the accumulation of CO_2 in the blood and tissues of the animal. This excess of CO_2 is supposed to cause a form of narcosis as seen in the torpid condition of the hibernating animal. When the CO_2 reaches a certain concentration the respiratory center is excited, respiration accelerated, and the muscles become hyper-irritable. These culminating results are responsible for the awakening from dormancy. The author claims that he can induce typical hibernating sleep by causing the active marmot to breathe a mixture of air (42 per cent), CO_2 (45 per cent) and oxygen (12 per cent). Torpid marmots remain dormant if supplied with this mixture. By increasing the proportion of CO_2 respiration is accelerated, and if the supplying of CO_2 is continued the hibernating marmot wakes up. The CO_2 is supposed to act principally on a nervous center for sleep situated in the mid-brain, since marmots deprived of cerebral hemispheres are able to sleep and wake up; but with only the medulla intact they are unable to awake. Further, Dubois[74] (1894) found that CO_2 actually accumulates in the blood during hibernation in the marmot and decreases again when the animal wakes up. Such an increase in the CO_2 content of the blood during hibernation has just been observed in this laboratory in case of the woodchuck (*Marmota monax*).[75]

Upon sufficiently good authority[76] to receive the serious consideration of such an author as Max Verworn,[77] certain ascetics of India, known as fakirs, are able to voluntarily go into a condition of almost suspended animation not unlike hibernation in some respects. While in this condition it appears that these fakirs may be buried three or four feet in the ground for days, or may be inclosed for six weeks without food and with but little air in a tight box which in turn is sealed up in some dark inner room.

When disinterred the body is cold and stiff with no signs
of any pulse, and apparently lifeless; but it revives with
no bad after-effects upon the application of warm water
to the head and after being manipulated for a quarter of
an hour.   Dubois emphasizes the fact that in order to
induce this state of trance, the fakirs make it a point to
breathe as little as possible.   This and much other in-
direct evidence is brought forward by this author in sup-
port of his carbonic auto-narcosis theory of hibernation.

Mosso[78] (1899) holds just the opposite view. He thinks
that winter-sleep is due to a condition of acapnia, or lack
of CO_2 in the system.

It is not strange that in this age of ductless glands and
internal secretions some theory should be brought for-
ward that would involve the ductless glands.   In 1905
Salmon[79] advanced the view that the pituitary body (hy-
pophysis cerebri) is a center for sleep and produces an
internal secretion which by virtue of some vasomotor or
autotoxic power acts on the nervous system and thus pro-
duces normal sleep. His view has been further elaborated
in later publications[80] (1910) in which he states that hi-
bernation may be explained upon an analogous mechan-
ism involving especially the so-called hibernating gland
—a structure which has lately received renewed attention
by physiologists. Salmon seems to favor the old idea
that a depletion of the cerebral blood vessels offers the
best explanation of the lethargy characteristic of the hi-
bernating state.   The rôle of the hibernating gland, how-
ever, is very uncertain. This structure is now generally
regarded as reserved food. Vignes[81] (1913), however,
considers it probable that it plays some important physi-
ological rôle, particularly in hibernation, since its ex-
tirpation in the white rat, where the operation is at-
tended with little difficulty, is nearly always fatal.   He
finds that this structure modifies the action of certain
toxic substances such as adrenalin, chloroform, tetanus
toxin and cobra venom, retarding the action of some and
accelerating that of others. He further maintains that

this gland contains lipase, and while it does not convert starch to sugar, its extirpation diminishes the amyloptic power of the serum. It also has an antitryptic power. Thus he conceives that it might serve as an economizer of proteins by insuring the utilization of reserve carbohydrate and fats during the long period of winter-sleep.

Salmon's view on the rôle of the hypophysis cerebri in the production of sleep was soon criticized by Gemelli[32] (1906), who argued that if this hypothesis were correct, the pituitary body would show signs of increased activity during hibernation, since, as has already been stated, hibernation is considered by many to differ from ordinary diurnal sleep only in degree and duration. But on the contrary, he found that the cyanophil cells of this gland in the marmot decreased during winter-sleep and that they increased again simultaneously with the appearance of numerous karyokinetic figures after the animal wakes up in the spring. Gemelli interpreted his findings as indicating that the anterior lobe of this organ cooperates with other ductless glands in neutralizing toxins which are produced in increased quantity when the animal becomes active, and hence is not to be regarded as a center of sleep. A later contribution to the relationship between the pituitary body and hibernation is by Cushing and Goetsch[82] (1913). As a result of observations on the hypophysis of the woodchuck, in which they confirm in general the findings of Gemelli on the decrease in size and histological changes during winter-sleep, these authors suggest that hibernation may be ascribed to a period of physiological inactivity, possibly of the entire ductless gland series, but certainly more especially of the pituitary gland, because during the dormant period this structure diminishes in size and shows profound histological changes and because deprivation of this gland in the human subject and in experimental animals causes a train of symptoms comparable to those of hibernation. Mann[83] (1916), however, found demonstrable changes in the pituitary body and other ductless glands of a large num-

ber of ground-squirrels (*Citellus tridecemlineatus*) to be absent or so inconstant, especially at the critical period— at the onset of hibernation—that the assumption of any theory ascribing the phenomenon of hibernation to a lack of function of all or any one of the ductless glands is not justified.

From this general summary it will be seen that great diversity of opinion prevails regarding the immediate cause of this extremely interesting condition, and of the sudden transformation from the homoiothermal to the poikilothermal state (and vice versa) so characteristic of hibernating mammals. It is not the author's object, however, to discuss the relative merits of the various theories. Suffice it to say that all of them are based upon insufficient data. To say which of the various conditions associated or occurring simultaneously with winter-sleep are concerned with the production of the lethargy and which are the results of this or some other condition, is extremely difficult. Until certain causal relations are definitely established between the factors concerned, many of these theories are of very little value except as a stimulus to further research. It is thus very evident that we are far from having any adequate explanation of the mechanism of this phenomenon, to say nothing of how it was established as a more or less variable character in certain animals.

If hibernation of mammals is only an extreme form of ordinary diurnal sleep of man and other animals, it is especially to be hoped that this subject will continue to be investigated by more modern and adequate means, for no entirely satisfactory theory has yet been advanced to explain the physiological cause of ordinary sleep. Since winter-sleep may also be attended with total abstinence from food and drink for many months, the facts derived from a study of the various conditions associated with this dormant period are of interest also in connection with the subject of inanition in particular and metabolism in general, as is plainly indicated by the frequent reference

to and comparison with the observations on hibernating animals found in the literature on inanition.

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SHORTER ARTICLES AND DISCUSSION

VARIATION, CORRELATION AND INHERITANCE OF FERTILITY IN THE MAMMALS

THE purpose of this review is to give an outline of the problems of fertility in the mammals (exclusive of man) which may be solved by the application of biometric formulæ to statistical data, to furnish an index to the available statistics, and to indicate the results to which the statistical analyses of the raw observations have led. Many of the biometric constants are published here for the first time.

TYPE AND VARIATION IN FERTILITY

The most fundamental biological questions which can be asked concerning series of data on fertility *considered quite independently of any other characteristic of the organism, its ancestry or its environment* are three:

(*a*) What is the typical and average fertility of different species or races?

(*b*) What is the variation, within the race, in reproductive activity as compared with that of variation in the degree of development of somatic characters?

(*c*) May fertility, like the bodily attributes of organisms, be described by mathematical curves?

With more comprehensive data concerning other characteristics of the individual organism, its ancestry or environment, more varied problems may be investigated, but none of more fundamental importance.

With respect to (*a*) it need only be said initially that biologically a knowledge of the number of offspring characteristic of a species has the same importance as a knowledge of any other of its peculiarities. That species may differ widely in fertility as in other characteristics is obvious without the collection of extensive statistics or the application of mathematical formulæ. It is only in a consideration of relatively *slight* differences in fertility in *nearly related* species or races or in individuals of the same race existing under various conditions, that biometric

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work became indispensable. It is just here, too, that the purely descriptive significance of fertility gives way to genetic, economic and sociological sources of interest.

As yet information on these subjects is all too meager. Lloyd[1] has emphasized slight differences in fertility in species formation in the rodents. Donaldson[2] has brought together the available data for fertility in the rat. For swine, Rommel[3] and Bitting[4] have given extensive data for different breeds and periods. Further records are available for swine from the studies of Wentworth and Aubel to be discussed below. Equations for theoretical curves of distribution of number of young per litter in Rommel's series have been worked out by Surface.[5] Large masses of statistics have been extracted from the herd books for sheep by Rietz and Roberts. Taken altogether, only a beginning has been made in a field that has not merely great biological interest, but in certain of its bearings is of material economic importance.

The most extensive and exact work on differences in fertility has been done on man, but a discussion of this subject falls outside the scope of the present review.

Since data for the solution of the problems of group (a) are as yet inadequate, it is idle to attempt any detailed discussion of those of group (b) and (c). Data for such purposes are, however, now becoming available much more rapidly than heretofore.

Birth Order and Litter Size

Fairly large series of records showing the relationship between birth order and litter size are now accessible.

Minot[6] has given data for the relationship in guinea pigs. The averages which may be computed from these are:

Order of Litter	F	Mean Size
First	51	1.96
Second	29	2.97
Third	15	2.80
Fourth	4	3.50

[1] Lloyd, R. E., "The Inheritance of Fertility," *Biometrika*, 8: 244–247, 1911.

[2] Donaldson, H. H., "The Rat," pp. 22–23, 1915.

[3] Rommel, G. M., "The Fecundity of Poland China and Durac Jersey Sows," Circ. U. S. Dep. Agr., Bu. Anim. Ind., 95, 1906.

[4] Bitting, A. W., "The Fecundity of Swine," Ann. Rep. Ind. Agr. Exp. Sta., 10: 42–46, 1897.

[5] Surface, F. M., "Fecundity of Swine," *Biometrika*, 6: 433–436, 1906.

[6] Minot, C. S., "Senescence and Rejuvenation," *Jour. Phys.*, 12: 97–153, 1891.

Crampe[7] many years ago showed from his extensive data on rats that the maximum fertility was on the second litter. King and Stotsenberg[8] have recently given data which lead to the following averages:

Order of Litter	F	Mean Size
First	21	6.24
Second	21	7.71
Third	18	7.06
Fourth	15	6.40

Pearson and Weldon have shown[9] that in mice there is an increase in the mean number of young from the first to the third litter, thus:

Order of Litter	Mean Offspring
First	5.46
Second	5.57
Third	5.76

For the rabbit Bailey, *fide* Hammond,[10] gives the values:

Order of Litter	Mean Offspring
First	5.58 ± 0.32
Second	7.25 ± 0.41
Third	7.08 ± 0.38

Such data as these are of obvious importance in the physiology of reproduction in the mammals. They will be of far greater value when it is possible to determine the influence of the actual age of the mother as well as of the order of birth upon fertility. Detailed records of size as well as of number of offspring and of mortality would also be of great importance.

RELATIONSHIP BETWEEN FERTILITY AND SOMATIC CHARACTERS

The interrelationship between fertility and somatic characters is a subject which may have a morphogenetic, genetic or economic interest.

Reference to some of the earlier literature has already been

7 Crampe, H., "Zucht-Versuche mit zahmen Wanderratten. I. Resultate der Zucht in Verwandschaft," *Landwirths. Jahrb.*, 12: 389–449, 1883.

8 King, H. D. and J. M. Stotsenberg, "On the Normal Sex Ratio and the Size of the Litters in the Albino Rat (*Mus norvegicus albinus*)," *Anat. Record*, 9: 403–420, 1915.

9 *Biometrika*, 7: 384, 1910.

10 Hammond, J., "On Some Factors Influencing Fertility in Domestic Animals," *Jour. Agr. Sci.*, 6: 263–277, 1914.

made[11] in a memoir dealing with plant materials and certain special problems more minutely analyzed on further sets of data.[12]

In the mammal, the relationship between fertility and somatic characters may be determined from (*a*) the somatic characters of an individual mother and her fertility, or (*b*) the characteristics of the progeny which serves as the measure of the fertility of a mother. Obviously, these two methods of operation are biologically not at all comparable.

The economic importance of the possible correlation between bodily characteristics and fertility has naturally given rise to many popular beliefs concerning the existence of such a relationship. Wentworth and Aubel[13] have, however, found no evidence of such in a comparison of the mean litter size in "large type" and "small type" hogs.

Pearson has shown[14] from Captain Lloyd's data[15] that there is a sensible and almost linear relationship between weight of mother and number of young in litter in Poona and Belgaum rats. The intensity of the correlation is, however, low, of the order $r = .160$.

Data for the full interpretation of such relationships are much needed but not as yet available. The problem is evidently one of great complexity. As Pearson points out, at certain stages of pregnancy the number of young might actually influence, by its own contribution, maternal body weight.[16] Furthermore, in these rodents growth continues notwithstanding pregnancy, and one might expect some correlation between weight of mother and size of litter as a resultant of the relationship between the age of the mother and her own weight and the age of the mother and the size of her litter.

Minot found that the over-gain in weight of pregnant guinea pigs is not all lost after delivery[17] and Watson[18] many years ago

[11] Harris, J. Arthur, *Biometrika*, 8: 52–65, 1910.

[12] Harris, J. Arthur, *Amer. Jour. Bot.*, 1: 398–411, 1914.

[13] Wentworth, E. N. and C. E. Aubel, *Jour. Agr. Res.*, 5: 1148, 1916.

[14] Pearson, K., ''Darwinism, Biometry and Some Recent Biology,'' I, *Biometrika*, 7: 368–385, 1910.

[15] Lloyd, R. E., ''The Relation between Fertility and Normality in Rats,'' *Rec. Ind. Mus.*, 3: 261–265.

[16] Minot (*Journ. Phys.*, 12: 141–145, 1891) has shown that in the guinea pig there is a relatively enormous over-gain in weight before delivery.

[17] Crampe (*loc. cit.*) has given certain data on the weight of mothers after the first and second deliveries in the rat.

[18] Watson, J. B., ''The Effect of the Bearing of Young upon the Body

adduced evidences to show that females which have borne young are heavier than unmated controls. Whether the effect of bearing young is cumulative in such a way as to influence the correlations in Captain Lloyd's series is not yet evident.

Taking these various factors into account, there seems little ground for believing that there is any material correlation between the fertility of a mammalian female and her measurable somatic characters.

There is an obvious physiological and morphogenetic interest attaching to the correlations between the number of individuals born in a litter and the characteristics of these individuals.

Consider first the correlations between number of pigs in the litter and number of nipples, in swine. For Parker's[19] and Bullard's data the values are:

$$\text{For males,} \quad r = .0810 \pm .0121,$$
$$\text{For females,} \quad r = .0324 \pm .0124.[20]$$

These are numerically low, but both are positive, and may possibly be significant in comparison with their probable errors. They may indicate morphogenetic relationships between the vigor of the mother as indicated by the number of her young and the characteristics of these young.

These positive correlations for number per litter and number of nipples are of interest in connection with the *negative* correlation for number in the litter and mean weight of individuals suggested many years ago by Minot,[21] who states that in guinea pigs the size of the animals at birth depends to a considerable degree upon the number of young in a litter: the larger the litter the smaller the animals at birth. Fortunately Minot has given data from which approximate[22] values of the correlation between number of individuals per litter and birth weight may be compared. The results are:

Weight and the Weight of the Central Nervous System of the Female White Rat,'' *Jour. Comp. Neur. Psychol.*, 15: 514–524, 1905.

[19] Parker, G. H. and C. Bullard, ''On the Size of Litters and the Number of Nipples in Swine,'' *Proc. Amer. Acad. Arts and Sci.*, 49: 399–426, 1913.

[20] Parker and Bullard give the correlation $r = .0035 \pm .0124$ for females only. This is evidently erroneous. Both values given here have been calculated from their data.

[21] Minot, C. S., ''Senescence and Rejuvenation. I. On the Weight of Guinea Pigs,'' *Jour. Phys.*, 12: 96–153, 1891.

[22] The only difficulty lies in the fact that his Tables VII and VIII do not contain the same number of individuals.

$$\text{For males,} \quad r_{nw} = -.437 \pm .039,$$
$$\text{For females,} \quad r_{nw} = -.431 \pm .044,$$
$$\text{For all,} \quad r_{nw} = -.430 \pm .029.$$

The results for males and females are in remarkable agreement. Evidently there is a large influence of the number born upon the weight of the individual.[23]

If the results be expressed in terms of regression of weight of individual upon number in litter the equations are:

$$\text{For males,} \quad w = 87.626 - 5.214\,n,$$
$$\text{For females,} \quad w = 84.375 - 4.741\,n,$$
$$\text{For all,} \quad w = 86.006 - 4.960\,n.$$

King[24] has given direct evidence for the influence of weight of mother in the weight of the young at birth.

Very young females and those that have passed their prime have smaller litters, as a rule, than females at the height of their reproductive powers.

And again,

The body weight of a female influences the birth weight of her young chiefly because it depends on the two more important factors of age and physical condition.

Finally it may be noted that in the case of sheep the size at birth and rate of development of twin and triplet as compared with the single lambs is a problem of very real economic importance. Both Bell and Marshall have considered this phase of the question. Unfortunately no extensive quantitative data are available for analysis on this point.

INHERITANCE OF FERTILITY

Biologically all recent studies on the inheritance of fertility differ from the classic memoir of Pearson, Lee and Branley-

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[23] That factors other than number per litter may profoundly influence birth weight may be seen at once by determining the correlation between the weight of the individual pigs born in litters of two as given in Minot's Table XI. Using symmetrical tables I find for the correlation between the weight of the two individuals

$$r_{w_1 w_2} = .686 \pm .046.$$

This similarity in weight is probably due in part to hereditary and in part to environmental factors.

[24] King, H. D., "On the Weight of the Albino Rat at Birth and the Factors that Influence It," *Anat. Rec.*, 9: 213–231, 1915.

Moore[25] on fertility in man and fecundity in race horses in that they deal with the number of young produced at a single birth instead of with the total young produced during the reproductive period or the ratio of the number of young actually born to the number which might have been produced under the circumstances.

For Poland China sows Rommel[26] and Rommel and Phillips[27] found values of the correlation between the size of litters in which dam was farrowed and size of litters produced by daughters ranging from .1088 to .0032, the values decreasing with moderate regularity as the daughters became older. For all ages they find the correlation $r = .0601$, and conclude that fertility is slightly but definitely inherited.

George (*fide* Wentworth and Aubel, *loc. cit.*) worked out four supplementary series in Poland China swine with the results:

Daughter and dam, $r = .0615 \pm .0390$,
Dam and grandam, $r = .1147 \pm .0343$,
Daughter and maternal grandam, $r = .0025 \pm .0392$,
Daughter and paternal grandam, $r = .0508 \pm .0392$.

All of these values are positive, but they are very small and no one of them may be considered statistically trustworthy in comparison with its probable error.

Weldon and Pearson[28] give a series of six relationships, both parental and grandparental, for size of litter in mice, with the result that no correlation whatever could be demonstrated.

Wentworth and Aubel[29] have considered the possibility of the segregation of litter size in the two first descendant generations of matings between boars and sows farrowed in litters of various sizes by determining the standard deviation of the number per litter in the so-called F_1 and F_2 generations. Let l be the num-

[25] Pearson, K., A. Lee and L. Branley-Moore, *Phil. Trans. Roy. Soc. Lond., A,* **192**: 257–330, 1899.

[26] Rommel, G. M., ''Inheritance in the Female Line of Size of Litters in Poland China Sows,'' *Biometrika,* **5**: 203–205, 1906.

[27] Rommel, G. M., and E. F. Phillips, ''Inheritance in the Female Line of Size of Litter in Poland China Sows,'' *Proc. Amer. Phil. Soc.,* **45**: 245–264, 1906.

[28] Pearson, K., ''On Heredity in Mice from the Records of the Late W. F. R. Weldon. I. On the Inheritance of the Sex Ratio and of the Size of Litter,'' *Biometrika,* **5**: 436–449, 1907.

[29] Wentworth, E. N., and C. R. Aubel, ''Inheritance of Fertility in Swine,'' *Jour. Agr. Res.,* **5**: 1145–1160, 1916.

ber of pigs in the litter in which an individual was farrowed, d the number of pigs in the litter in which its dam was farrowed, and S and D the numbers in the litters in which the grandsire and grandam were farrowed. Then, the authors reason, if fertility be due to factors which differ in the grandsire, S, and the grandam, D, and if Mendelian segregation occurs in the fashion assumed by several of these who have worked on quantitative characters, one should expect the mean value of the standard deviation of litter size in cases in which D and S differ widely to be higher than the mean value in cases in which they are closely similar. There is no conclusive evidence of such greater segregation in the F_2 from dissimilar grandparents.

Now the data published by Wentworth and Aubel permit the consideration of several additional questions of considerable interest in connection with the problem of the inheritance of fertility. Thus from the mean litter sizes in their Table II and the distributions of litter size in the three generations in their Table IV, it is quite possible to calculate *approximately*[30] correct correlations for the relationship between size of litter in different generations. Thus the formula:

$$r_{xy} = \frac{\Sigma(xn\bar{y}_x) - [\Sigma(x)/N][\Sigma(n\bar{y}_x)/N]}{\sigma_x \sigma_y},$$

where the bars denote the means of the y (descendant) litters associated with particular, x, classes of ascendant litters, leads to the values:[31]

$$r_S = .071 \pm .023, \quad r_{Dd} = .126 \pm .022,$$
$$r_{Sl} = .120 \pm .022, \quad r_{Dl} = .100 \pm .022.$$

Superficially considered, these values seem in excellent agreement with those published by Rommel and others, but the fact that r_{Sl} has a value which is possibly significant statistically, should at once arouse suspicion, for surely there is no genetic reason (excepting possibly non-viability of sperm or the production of duplicate twins through an influence of the sperm upon the egg) why there should be a correlation between the size of the litter in which a boar was farrowed and the size of litter in which his daughter was farrowed. Mistrust is heightened by the fact

[30] Unfortunately there are inconsistencies in these tables which show the existence of typographical errors precluding exact constants.

[31] Unfortunately data for the determination of r_{di} are wanting.

that r_{sd} is actually though perhaps not significantly lower than r_{sl}, whereas on the female side $r_{Dd}r > r_{Dl}$. Obviously there is no genetic reason for a correlation between the size of the litters in which the grandsires, *S*, and the grandams, *D*, were farrowed. But columns 1–3 of Table II of Wentworth and Aubel actually give:

$$r_{SD} = .121 \pm .022,$$

a value quite as large as those recorded above.

Such a correlation might arise (*a*) through the existences in the pens of different breeders of strains slightly differentiated with respect to fertility, (*b*) through differences in the conditions in which different breeders maintained their pens, providing such conditions affect litter size, or (*c*) through actual dishonesty of certain breeders in reporting the size of litters for herd-book publication.

Such differentiation, if it exists, would also account in part at least for the correlations hitherto regarded as due to inheritance. The whole problem is evidently one of great complexity and requiring far more detailed investigation than it has yet received.

The problem of the inheritance of the production of twins in sheep which has been studied experimentally by Alexander Graham Bell for the past several years, has recently been investigated statistically by Rietz and Roberts.[32]

There seems to be unmistakable evidence of inheritance, or at least of ascendant influence,[33] upon descendant characteristics. This may be most clearly seen by comparing the average number per litter resulting from certain matings.

Thus for the parental relationship the results are:

When sire and dams are singles .... 1.3452 ± 0.0059
When sire is single and dam is twin .... 1.4171 ± 0.0067
When sire is twin and dam is single .... 1.3946 ± 0.0073
When sire is twin and dam is twin .... 1.4548 ± 0.0088
When either sire or dam is a triplet .... 1.6076 ± 0.0300
  Mean of all offspring .... 1.3979 ± 0.0035

[32] Rietz, H. L. and E. Roberts, ''Degree of Resemblance of Parents and Offspring with Reference to Birth as Twins for Registered Shropshire Sheep,'' *Jour. Agr. Res.*, 4: 479–510, 1915.

[33] In the case of slight relationships between parents or earlier ancestors and offspring there is always danger of attributing to heredity the influence of purely physiological factors.

Or for the dams and grandams:

When dams and grandams are singles .... 1.3446 ± 0.0057
When the dams are singles and grandams twins .... 1.3689 ± 0.0070
When the dams are twins and grandams are singles....... 1.4245 ± 0.0071
When the dams are twins and grandams are twins .... 1.4559 ± 0.0078
When either dam or grandam is a triplet .... 1.545 ± 0.037

Finally for the maternal grandams alone:

When the maternal grandams are singles .... 1.3784 ± 0.0045
When the maternal grandams are twins .... 1.4120 ± 0.0052
When the maternal grandams are triplets .... 1.556 ± 0.033

It is quite out of the question to review in any detail the thorough analysis of the numerous interrelationships deduced from the many thousands of records abstracted by the authors from the Shropshire record. Their data seem to be free from the possible objection raised against the swine records above, for the correlation between sire and dam, which may be deduced from their Table I, is only $r = .0058 ± .0070$.

The intensity of correlation between the size of litter in which an individual is born and the size of the litter in which his sire or dam or grandsire or grandam was born is very low. The maximum relationships are in fact of the order $r = .08$.

In the parental relationships the correlation between the size of litter in which the sire was born and the size of the litter in which his offspring were born seems to be significant, as well as that between the size of the litter in which the dam was born and the number of the offspring. The mean number of offspring are:

When the sire was born single .... 1.3787 ± 0.0045
When the sire was a twin .... 1.4220 ± 0.0057
When the sire was a triplet .... 1.683 ± 0.045

Note the agreement of this result with that obtained by Wentworth and Aubel. An explanation on the basis of identical twins induced by the characteristics of the sperm, or of partial impotency in certain males, should be sought by those who have experimental facilities.

There seems to be a significant correlation between maternal

grandams and offspring, but it is impossible to assert any trustworthy correlation for the other grandparents.

INFLUENCE OF ENVIRONMENT ON FERTILITY

Marshall[34] while emphasizing the importance of the hereditary factor in multiple births in sheep, adduces evidences for the great importance of feeding as a factor in the production of twins and triplets. His figures certainly show great and consistent differences in the produce of flocks which have received different treatment at and preceding tupping time. Unfortunately differences in breed may, but do not necessarily, cast some doubt on the interpretation of the data. The problem which he has attempted to solve by the analysis of schedules received from flock masters certainly deserves experimental study. Such investigations have actually been begun by Evvard who in a first[35] and second[36] and third[37] report on experiments with swine has given the results of various feeding upon the vitality of the offspring. Discussion of the data as they are presented in these papers falls outside the scope of a biometric review. Such work is, however, of great importance at a period of science in which heredity as contrasted with environment is apt to be assumed to be an all-important factor. It is a pity that such experiments as these of Marshall and Evvard can not be carried out in close cooperation with experts on the physiology of nutrition, so that differences in rations might be arranged on a uniform scale.

<div align="right">J. ARTHUR HARRIS</div>

ON A BARNACLE, CONCHODERMA VIRGATUM, ATTACHED TO A FISH, DIODON HYSTRIX[1]

A SPECIMEN of the "sea porcupine," *Diodon hystrix* Linn., seen swimming near the surface and secured with a dipnet, was

[34] Marshall, F. H. A., "Fertility in Scottish Sheep," *Trans. High. Agr. Soc. Scotland*, V, 20: 139–151, 1908.

[35] Evvard, J. M., "Nutrition as a Factor in Fetal Development," *Proc. Amer. Breed. Ass.*, 8: 549–560, 1912.

[36] Evvard, J. M., "Some Factors affecting Fetal Development," *Proc. Iowa Acad. Sci.*, 20: 325–330, 1913.

[37] Evvard, J. M., A. W. Dox and S. C. Guernsey, "The Effect of Calcium and Protein Fed Pregnant Swine upon the Size, Vigor, Bone, Coat and Condition of the Offspring," *Proc. Iowa Acad. Sci.*, 21: 269–278, pl. 31–35, 1914.

[1] Contributions from the Bermuda Biological Station for Research, No. 50.

found to have two living lepad barnacles attached to one of its erectile spines[2] upon the ventral surface two centimeters to the right anteriad of the anus. The *Diodon* was a small individual, 16 cm. long. It was kept under observation in the laboratory for several weeks.

According to a determination for which I am indebted to Mr. H. G. Coar, the barnacles belong to the species *Conchoderma virgatum* (Spengler), although varying "a trifle from Gruvel's type description, but not sufficiently to correspond to *Conchoderma hunteri* R. Owen, 1830, which the specimen approached slightly, nor to Leach's (1818) variety *chelonophilus* of *C. virgatum*." This species has not previously been recorded from the Bermuda area, though it is known over the Atlantic generally and (to judge from statements of fishermen) occurs here upon young turtles. *C. virgatum* has been found on *Mola*, ships' bottoms, and various other objects (Pilsbry, 1907, p. 99), but the present record is somewhat unusual.

Different semiparasitic lepads have quite various hosts, such as medusæ, antipatharians, the spines of echinoids, molluses, crustaceans, sharks, teleosts, turtles, the tail feathers of sea birds, whales, and so forth (Pilsbry, 1907; 1910). Those occurring on fishes seem, naturally, to affix themselves to some hard part, for example, the head, as in the case of *Tylosurus* (Sumner, Osburn, and Cole, 1913, p. 647). Jordan (1905, p. 341, fig. 226) figures a flying fish with conchodermas attached to a *Penella* growing on the fish, a condition of double parasitism which has been described for Xiphias. In the present instance, the larger of the two conchoderma individuals (20 mm. long) was found to have its peduncle completely surrounding the spine to which it had become fixed. The second individual was much smaller (4 mm. long) and attached to the peduncle of the first. Both specimens were so oriented that the opening between the valves was directed toward the head of the fish. The skin of the fish about the base of the spine was inflamed, and the muscles which normally control its elevation for defensive purposes had apparently degenerated. When it was attempted to preserve the *Diodon*,

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[2] The figure of *Diodon hystrix*, which is used in current ichthyological handbooks, represents the animal in a semipuffed-up condition and with the frontal spines erected. Alive, the fish has a quite different aspect, all the spines being flattened down to the skin unless the creature is much disturbed. When preserved in formalin it assumes the appearance depicted in the handbooks.

the spine bearing the conchodermas became detached in the
course of the animal's self-inflation. It is probable, therefore,
that the spine would soon have been shed under natural circum-
stances.

Several features of the behavior of these conchodermas are of
interest in comparison with those of other barnacles. Some years
ago it was reported by Pouchet et Joubert (1876) that cirripedia
attached to rocks reacted to shading, while those attached to
floating objects did not; their inference being that to the station-
ary barnacles a shadow signified danger, whereas, to those borne
about at the surface of the water, a fluctuating illumination was
the normal state of affairs. This observation has been regarded
as an instance of adaptation comparable with that of Hargitt
(1909) on the gradual loss of reaction to shading when serpulids
are maintained in the laboratory.

The specimens of *Conchoderma* attached to *Diodon* did not re-
act to shadows under any of a number of experimental condi-
tions. They seem, therefore, to be in agreement with the obser-
vation of Pouchet et Joubert. But tests upon lepads found upon
floating timbers and upon *Ascophyllum* showed that *Lepas
anserifera* and *L. pectinata* do respond to shading by retracting
the legs and approximating the valves. From a number of tests
it appeared that neither the legs nor valves are sensitive to shad-
ing, but that the shadow must affect some part of the body within
the shell suggesting that the persisting nauplius eye is the
organ involved. The extent of the response varies with the de-
gree to which the appendages have been extruded: when just
being extruded, they react by complete retraction; when fully
extruded, by a partial retraction; after being fully extruded for
one or two minutes, they react to shading quite promptly and
completely. After completion of a response there must usually
elapse from two to four minutes before another reaction can be
secured.

It seems to me, then, that the supposed adaptation of floating
barnacles is not of the nature which has been supposed. Whether
the non-reaction of *Conchoderma* to shading is properly to be
considered a direct adaptation is therefore questionable. The
host of these particular specimens is not a surface fish, and the
absence of sensitivity to shading may be due to their deep
habitat. Direct sunlight inhibited the rhythmic movements of
the conchodermas, and they were much more active at night than
in diffuse laboratory light.

The statement is occasionally met with that in barnacles attached to a free-swimming animal the feathery feet are merely thrust out, not waved about as in the rock barnacles, which must create food- and respiratory-currents for themselves. Now, it was observed that when the *Diodon* bearing the conchodermas was actively swimming, the legs of the lepads remained extended for as much as four to five minutes; whereas, when the fish remained stationary, they were alternately extended and retracted about seven times every minute (at 18° C.), the extension in the latter case being not so great as when their host was moving. *Lepas anserifera* and *L. pectinata* were then tested as to their behavior in currents, with this result: when the wood to which they were attached was stationary, the rhythmic contraction of the appendages was continuous, but if a gentle stream of water from a supply jet was allowed to flow past them impinging on the anterior (concave) edges of the legs, they remained extended for as long as ten minutes, and were spread farther apart than in the absence of the current. This was not due to any merely mechanical effect of the water stream, as the feet could at any time be caused to contract at a touch. A water stream, striking the posterior (convex) edges of the legs, led to contraction and subsequent limited extrusion of these appendages. A more correct interpretation of the phenomenon described in floating barnacles seems to be, therefore, that when the concave side of the appendages is stimulated by a water current, the animal responds by pushing out its legs further than is usual in the absence of currents, while their rhythmic contraction is inhibited. It should be noted that the two specimens of *Conchoderma* observed were so oriented on the *Diodon* as to receive the full benefit of currents derived from its forward swimming; and further, that this fish is not a vigorous swimmer, so that the currents in question are by no means rapid, but rather such as could be efficiently strained by the barnacles.

W. J. CROZIER

AGAR'S ISLAND,
BERMUDA

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